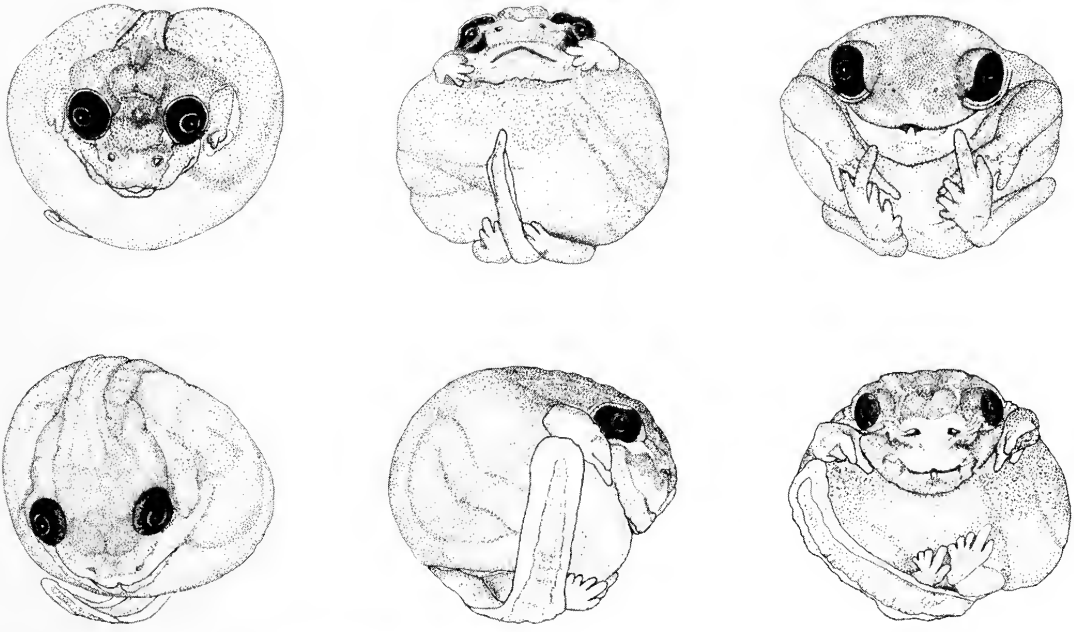
ISSN 0312 3162

Records of the Western Australian Museum



Volume 23 Part 3 2007

Records
of the
Western Australian Museum

The *Records of the Western Australian Museum* publishes the results of research into all branches of natural sciences, and social and cultural history, primarily based on the collections of the Western Australian Museum and on research carried out by its staff members.

Collections and research at the Western Australian Museum are centred on Earth and Planetary Sciences, Zoology, Anthropology, Archaeology and History. In particular the following areas are covered: systematics, ecology, biogeography and evolution of living and fossil organisms; palaeontology; mineralogy; meteoritics; anthropology and archaeology; history; maritime history and maritime archaeology; and conservation.

Western Australian Museum
Perth Cultural Centre, James Street, Perth, Western Australia 6000
Mail: Locked Bag 49, Welshpool DC, Western Australia 6986
Tel. (08) 9212 3700
Fax. (08) 9427 2881
E-mail reception@museum.wa.gov.au

The *Records of the Western Australian Museum* is published approximately three times per year. A series of *Supplements* is also produced. The *Records* are available for sale and exchange, the current price being $11 plus postage per part. Each volume comprises four parts. Subscriptions can be taken out for whole volumes at a rate of $33 plus postage. Supplements can be purchased from the W.A. Museum Bookshop. Prices on request. Prices include GST.

Printed and published by the Western Australian Museum

ISSN 0312 3162

Cover: Sample developmental stages for the direct developing frogs *Arenophryne rotunda* (row 1) and *Myobatrachus gouldii* (row 2).

Records of the Western Australian Museum **23**: 213–217 (2007).

A new species of *Gnathoxys* (Coleoptera: Carabidae: Carabinae) from an urban bushland remnant in Western Australia

Nadine A. Guthrie

Department of Environment and Conservation, Wildlife Research Centre,
PO Box 51, Wanneroo, Western Australia 6946, Australia
Email: Nadine.Guthrie@dec.wa.gov.au

Abstract – *Gnathoxys pannuceus* sp. nov. is described and illustrated from a specimen collected from Woodman Point Reserve, Western Australia. It is distinguished from other *Gnathoxys* species by the highly distinctive wrinkled pattern on the elytral surface, a feature that immediately distinguishes it from all other members of the genus.

INTRODUCTION

The ground beetle genus *Gnathoxys* Westwood 1842 is endemic to Australia and 16 species are currently recognised. The majority of these species occur in the southwestern region of Western Australia and seven occur along the Murray-Darling River system (Moore *et al.* 1987). *Gnathoxys punctipennis* Macleay 1873, also occurs along the southern coastal regions between southwest Western Australia into the South Australian Gulf region. Two species have not been seen since initial collection: *G. irregularis* Westwood 1842, reported from Port Essington in the Northern Territory by Westwood (1842) and *G. sulcicollis* Sloane 1910, from central Australia (no type locality was reported for this species; Moore *et al.* 1987).

Since initial collection, little has been determined about the ecology, taxonomic relationships or distributions of the various species within *Gnathoxys*. Generic relationships are not clear; however, Macleay (1864) suggested tentative associations between *G. tesselatus* Macleay 1864 and *Promecoderus* based upon the dilation of the male fore tarsus. Roig-Juñent (2000) however, determined that within the Broscitae, *Gnathoxys* forms a natural grouping with the other Australian endemic genera *Cerotalis, Adotela* and *Brithysternum* and is only distantly related to other genera (including *Promecoderus, Creobius* and *Cascellius*) within the subtribe Creobiina of the Broscitae. *Gnathoxys* is unique among this group and is defined by possessing fore tibia with two medial teeth, fore and middle tibia markedly palmate, and maxillary and labial palpal apical segments of males securiform (Roig-Juñent 2000).

The broscitines are diverse and medium sized ground-dwelling beetles distributed in temperate, subarctic and subantarctic regions of the world, and are generally absent from the tropics (Davidson and Ball 1998). Within Australia, the group is an important element in the beetle fauna of arid areas (Matthews 1980). There are 11 recognised Australian genera, with all species endemic, but two genera are represented by other species outside of Australia (Moore *et. al.* 1987).

A recent survey of urban bushland remnants in Perth, Western Australia surveyed a number of sites in the metropolitan area and a large number of carabid specimens, including several species of *Gnathoxys*, were collected in pitfall traps (How *et. al.* 1996; Guthrie 2001). Amongst these samples was a single representative of an unusual new species of *Gnathoxys* collected from Woodman Point, south of Perth. The distinctive appearance of the elytral sculpturing of this specimen is sufficient to suggest that this represents a new species, and the species is named and described in this paper.

MATERIALS AND METHODS

The specimen was collected using wet pitfall traps along a 100 metre transect set with an ethylene glycol mix (400 ml of 70% ethylene glycol, 30% water). The specimen was stored in 75% ethyl alcohol until identification and removal of the genitalia, and then pinned. The specimen is lodged in the Western Australian Museum, Perth (WAM).

Measurements were taken using a stereo microscope with vernier callipers and expressed in millimetres. Body length was measured from the apical margin of the labrum to the apex of the elytra (T-L). Length of pronotum was taken along the midline (P-L). Fore tibia length was measured from the femur joint to tip of 1st tibial tooth (FT-L).

The gross genital morphology was examined by relaxing the specimen in a mixture of soapy distilled water and 2% acetic acid. The genitalia were then dissected out and cleared overnight in

cold 10% potassium hydroxide. Once cleared, the pH of dissected parts was neutralised in dilute acetic acid. The dissected male genitalia were placed in glycerine for examination (Liebherr 1990).

SYSTEMATICS

Family Carabidae

Subfamily Carabinae

Tribe Broscitae

Genus *Gnathoxys* Westwood, 1842

Type species

None designated by Westwood, but originally included nominotypical species: *Gnathoxys granularis* Westwood, 1842; *Gnathoxys irregularis* Westwood, 1842. *Gnathoxys granularis* Westwood, 1842 by subsequent designation of Roig-Juñent (2000).

Gnathoxys pannuceus, sp. nov.

Figures 1–7

Material examined

Holotype

Male, Woodman Point Reserve, Western Australia, site WP2 [32°07'50"S 115°45'28"E], wet pitfall trap, 4 November 1994–19 January 1995, collected by J. M. Waldock and M. S. Harvey (WAM #38293).

Diagnosis

Gnathoxys pannuceus is similar in overall appearance and size to *G. crassipes* Sloane but is distinguished from all other *Gnathoxys* species by being heavy in appearance with a large head relative to overall size. The pronotum is strongly globular in shape with a distinct medial sulcus and faint wrinkles on the otherwise smooth dorsal surface. The pronotum and elytra margins have fine long setae in greater abundance than other similarly sized *Gnathoxys*. The most obvious character that separates this species from all others in the genus is the striking elytral pattern. Whereas *G. granularis* has distinct granulated areas on the elytra, and other *Gnathoxys* species possess elytral patterns consisting of foveae, punctures or similar depressions, this species has a highly distinctive wrinkled pattern.

Description

Male (holotype) (Figures 1, 2)

Total length = 13.3 mm; elytral length/width = 7.6/5.9 mm; pronotum length/width = 4.3/5.1 mm; head length = 3.0 mm; fore tibia length = 2.9 mm. Colour entirely black without bronze or olive sheen, with dark orange eyes.

Figure 1 Dorsal habitus of *Gnathoxys pannuceus* holotype; male total length 13.3 mm

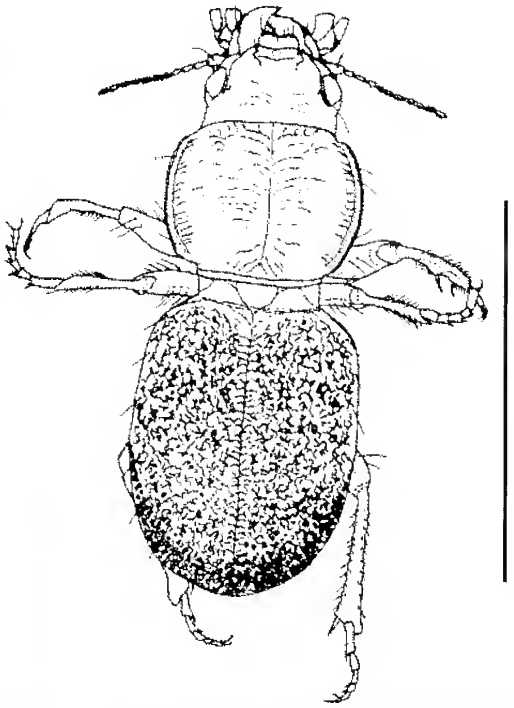


Figure 2 Detail of dorsal view of *Gnathoxys pannuceus* holotype; scale bar = 10 mm

Head. Very long, heavy mandibles approximately 2/3 of head length, slightly curved downward. Inner mandible edge straight and toothless, curved toward apex with deep overlap of mandible apices. Mandibular groove wide and shallow, approximately half mandible length, mandibular ridge very narrow. Single seta at groove apex and non-setiferous puncture on outer curve of mandibles near apex. Single seta on medial surface of 2nd segment of palp and on ventral surface of basal segment of maxilla palp. Maxillae and labial apical palp segments securiform. Two fine setae on anterior mentum medial margin and one on either side of extremities of basal maxilla. Labrum slightly broader than long, bifid and rounded. Medial sulcus extremely faint. A fringe of setae on under side of labial anterior margin and three pairs of setae on labial dorsal anterior margin. Outer labrum edges yellow with remainder reddish brown. Eyes round, convex and not prominent or overly large. Antenna short, moniliform with single seta on scape and segments 4–11 covered dorsally and ventrally with thick short setae. Supraorbital seta posterior to eye, with supraorbital sulcus running forward, terminated posterior to mandibular ridge. Deep latero-medial sulcus on either side of head, initiated in line with anterior half of eye, extended directly forward to lateral extremities of clypeus. Clypeus medially and anteriorly depressed, with one mid and two lateral creases medially aligned.

Prothorax. Pronotum very rounded, sub-spherical with very weak extensions at cervical collar insertion point. Narrow pronotal margin with setae in anterior and posterior third of margin. Medial sulcus extended forward to anterior margin. Lateral wrinkles traverse pronotum surface, strongest near medial sulcus, lateral margins and towards thickened and blunt basal margin. Prosternum with wrinkles around sparse cluster of setae in front of each leg (widest anteriorly), wrinkles continue onto proepimeron, tubercles reduced to slight swollen areas between anterior coxa.

Pterothorax. Elytra are sub-quadrate, slightly longer than broad with rounded sides and apex. Peduncle thick and short with heavy shoulders projecting. Elytral margin very thin, with five setae evenly spaced along anterior two thirds of margin. Apical declivity finely granulated, extending over posterior one sixth of elytra. Granulations extending along lateral margins, diminished anteriorly. Four setae evenly spaced along dorsal edge of apical declivity on each elytron. Dorsal surface of elytra finely creased and wrinkled with extremely irregular sulci, reminiscent of "crumpled aluminium foil re-flattened" (Figure 3).

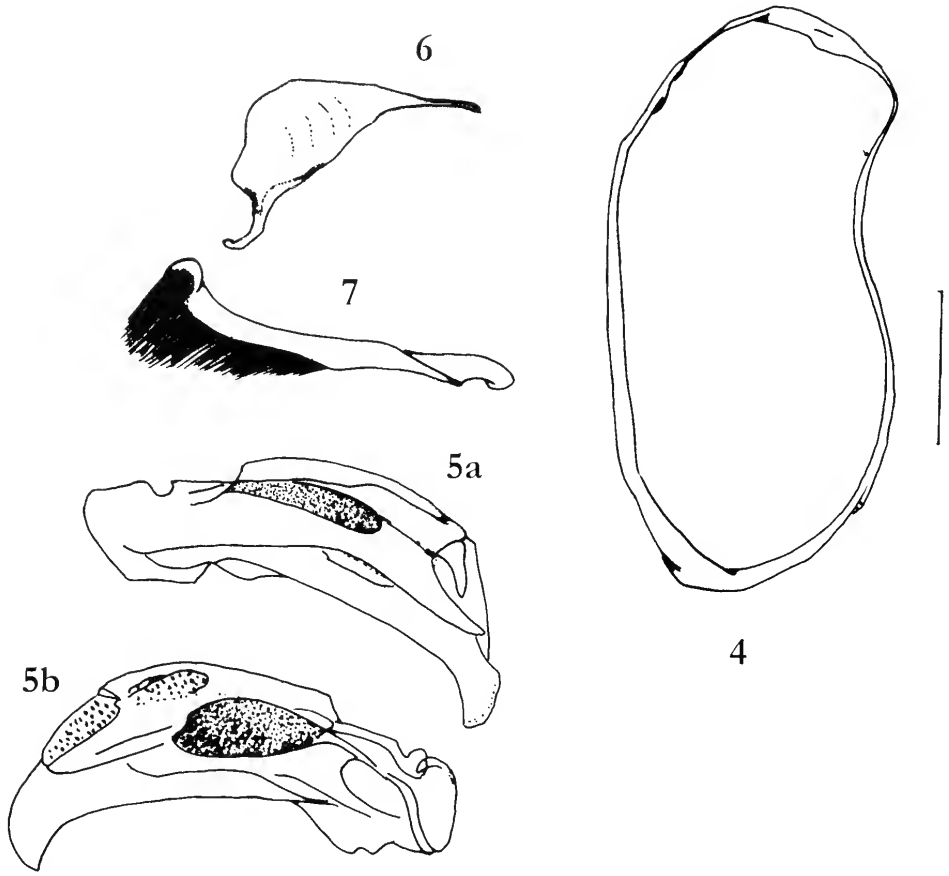
Abdomen. Ventrites bipunctate medially, with final seta pair positioned on medial portion of apical margin.

Legs. Foreleg: Trochanter ventral surface with one punctate seta. Femur with one cluster of setae on anterior ventral edge, two setae on posterior ventral edge, three setae on centre of posterior dorsal edge and a cluster centrally positioned on dorsal surface. Two teeth present on outer fore tibial edge, medial one smaller, both with a seta positioned on posterior distal margin. Linear arrangement of three setae along midline in line with antennal cleaning organ. A row of fine setae along inner edge of tibia terminated at cleaning organ. Rounded, flattened apical tooth directed distally. Tarsomeres triangular with outer lateral edge extended, narrowed distally towards 2nd tarsomere. Three or four stiffened setae on both tarsomere edges. Apical tarsomere filiform with 2 setae on lateral edges, tipped with symmetrical short curved claws.

Figure 3 *Gnathoxys pannuceus* sp. nov. Detail of apical elytral surface showing extremely irregular sulci.

Midleg: Coxae with a cluster of setae on anterior surface, one seta on ventral surface, and one ventrally on trochanter. Clusters of setae present on anterior, dorsal and posterior femoral surfaces. Femur widened dorso-ventrally. Tibia with linear rows of stiff setae orientated distally on anterior and posterior surfaces. A triangular apical tooth with stiffened setae forming a fringe around distal surface of tibia at tarsus insertion point. Two similar sized apical teeth inserted below tarsus. Tarsal arrangement identical to foretarsus.

Hindleg: Coxae with two setae on apical and basal margins. Cluster of setae on posterior and dorsal surfaces of trochanter. Long setae in curved linear clusters on posterior and ventral surfaces of femur. Long setae sparsely distributed on distal ventral and dorsal third of femur. Tibia elongate, flattened with widened distal end. Rounded apical tooth on tibia broad and short. Tibia edge serrated weakly, serrations with rounded points. Stiffened short setae in linear rows thickly cover tibial surfaces.



Figures 4–7 *Gnathoxys pannuceus* sp. nov. 4, genital ring; 5a, right (dorsal) view median lobe; 5b, left (ventral) view median lobe; 6, left paramere; 7, right paramere; scale bar = 1 mm

Shortened apical teeth, equal in length set below tarsal insertion point. Tarsal arrangement identical to anterior tarsus.

Male Genitalia. Genital ring ovoid in shape, with slight concavity towards basal third, and thin edges and no extensions (Figure 4). Median lobe (Figure 5a,b) thick, with no curvature and a small hook at apex. Orifice dorsally placed behind apex. Left and right sides of median lobe not symmetrical, with left (or ventral view) extended on upper surface near orifice. Parameres dissimilar (Figures 6, 7), left with extension on inner edge, extended to apical third of paramere. Right paramere larger and thicker, with thick setal brush extended from apex to mid-length, almost equal to adeagus in length.

Female: Unknown.

Etymology

The specific epithet is derived from the Latin adjectival *pannuceus* (lesser ragged, wrinkled, shrivelled) pertaining to the characteristic dorsal surface of the elytra.

Remarks

Gnathoxys pannuceus sp. nov. was collected from the type locality at Woodman Point and, although the pitfall traps were left open for twelve months, only a single specimen was collected. Searches at the type locality during the same season over several years have failed to locate any further specimens, suggesting that this species is locally uncommon or inhabits a microhabitat that is not effectively sampled through pitfall traps.

Numerous unidentified forms of *Gnathoxys* exist in collections (Western Australian Museum, Agriculture W.A. and the Australian National Insect Collection; author's unpublished observations). Sloane (1898) listed several unidentified *Gnathoxys* specimens but his descriptions and comments are too brief to satisfactorily ally any of the descriptions with these unidentified forms. It is also highly likely that more species of *Gnathoxys* will be collected in poorly surveyed areas of southwestern Australia. Therefore, a comprehensive revision of the genus

incorporating all available material, including currently undescribed forms and the old types is required immediately.

ACKNOWLEDGEMENTS

I thank M.S. Harvey and J.M. Waldock for access to the carabid specimens collected during the Ground Fauna of Urban Bushland Remnants in Perth Survey. Thanks also to T. Houston, A. Szito and T. Weir for access to carabid beetle collections at the Western Australian Museum, Department of Agriculture, WA and Australian National Insect Collection, Canberra. I also thank B.P. Moore for bringing to my attention the significance of this unusual specimen. Jane McRae kindly photographed the holotype for me. Finally, I thank my supervisors, Pierre Horwitz (Edith Cowan University) and Mark Harvey for their unending advice and support throughout this project.

REFERENCES

Davidson, R.L. and Ball, G.E. (1998). The tribe Broscini in Mexico: *Rawlinsius papillatus*, new genus and new species (Insecta: Coleoptera: Carabidae) with notes on natural history and evolution. *Annals of the Carnegie Museum* **67** (4): 349–378.

Guthrie, N.A. (2001). Aspects of the Taxonomy and Ecology of Ground Beetle (Carabidae) Assemblage on the Swan Coastal Plain (with particular reference to habitat fragmentation on the Quindalup Dune System). Masters Thesis, Edith Cowan University.

How, R.A., Harvey, M.S., Dell, J. and Waldock, J.M. (1996). *Ground Fauna of Urban Bushland Remnants in Perth*. Unpublished Report to the Australian Heritage Commission.

Liebherr, J.K. (1990). A new tribal placement for the Australasian genera *Homethes* and *Aeolodermus* (Coleoptera; Carabidae: Odacathini). *Pan-Pacific Entomologist* **66** (4):312–321.

MacLeay, W.J. (1864). On the scaritidae of New Holland. 2nd paper. *Transactions of the Entomological Society of New South Wales* **1**: 134–154.

MacLeay, W.J. (1873). Miscellanea entomologica. *Transactions of the Entomological Society of New South Wales* **2**: 319–370.

Matthews, E.G. (1980). *A guide to the genera of Beetles of South Australia. Part 1 Archostemata and Adephaga*. Special Educational Bulletin Series South Australian Museum, Adelaide.

Moore, B.P., Weir, T.A. and Pyke, J.E. (1987). Rhysodidae and Carabidae. Pp20–320. *In* D.W. Walton (ed). *Zoological Catalogue of Australia*. Volume 4. Coleoptera: Archostemata, Myxophaga and Adephaga, 444pp. (Canberra: Australian Government Publication Service).

Roig-Juñent, S. (2000). The subtribes and genera of the tribe Broscini (Coleoptera: Carabidae): cladistic analysis, taxonomic treatment, and biogeographical considerations. *Bulletin of the American Museum of Natural History* **255**: 1–90.

Sloane, T.G. (1898). On Carabidae from West Australia sent by Mr A. M. Lea (with descriptions of new genera and species, synoptic tables, etc). *Proceedings of the Linnean Society of New South Wales* **23**: 444–520.

Sloane, T.G. (1910). Studies in Australian Entomology. No. XVI New species of Carabidae. *Proceedings of the Linnean Society of New South Wales* **35**: 378–406.

Westwood, J.O. (1842). On the Scaritideous beetles of New Holland. Pp 81–90 pl. 24 *In* J.O. Westwood. *Arcana Entomologica* or illustrations of new rare and interesting insects. London : Smith Vol 1 iv 192 pp.

Manuscript received 29 April 2005; accepted 10 July 2006

Records of the Western Australian Museum **23**: 219–234 (2007).

Observations of the biology and immature stages of the sandgroper *Cylindraustralia kochii* (Saussure), with notes on some congeners (Orthoptera: Cylindrachetidae)

Terry F. Houston

Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia
Email: terry.houston@museum.wa.gov.au

Abstract – Field and laboratory observations of *Cylindraustralia kochii* are presented with notes on some congeners. Nymphs and adults create galleries in moist soil by compression of the soil with their powerful fore legs, burrowing to depths of up to 1.9 m. During the cooler months and 1–2 days after rain, sandgropers commonly burrow long distances close to the soil surface producing conspicuous raised trails. Adults and nymphs of various sizes were found throughout the year. Eggs and early immatures of the genus (and family) are described for the first time. Pedicellate eggs of *C. kochii* were suspended singly in closed chambers 40–190 cm deep in moist soil. A 'larval' stage hatches from the egg and moults to a first instar nymph while still in the egg chamber. Five nymphal instars are indicated by morphometric and morphological data. Eggs are laid from autumn to spring but hatching was only observed in mid summer. A duration of at least 12 months is indicated for first instar nymphs, so the complete life cycle may extend over several years. Examination of gut contents revealed that sandgropers are omnivorous, consuming a wide array of plant, fungal and arthropod material. Plant food included root, stem, leaf, flower and seed tissue. Cannibalism occurred in one very dense population of *C. kochii*. Otherwise, no insect predators or parasitoids were encountered. Associated organisms included gregarines and *Amoeba* (Protista) in the intestines, rhabditid nematodes in the genital chambers of adults, and six species of mesostigmatid and astigmatid mites which adhered externally to the body. Nymphs and adults produce an odorous, probably defensive secretion from a pair of abdominal glands.

Key words: subterranean insects, ethology, ecology, parasites

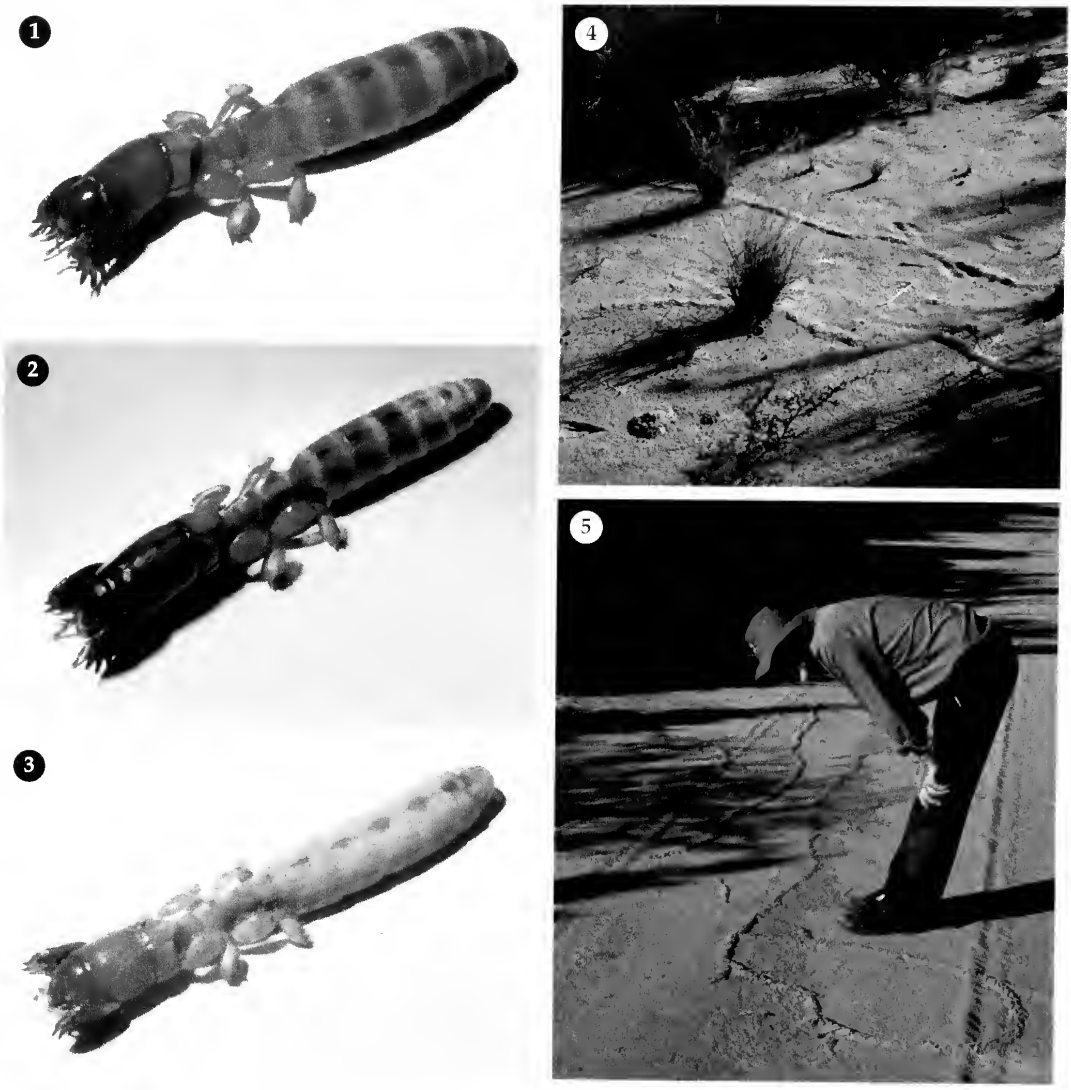
INTRODUCTION

Sandgropers, once regarded as degenerate mole crickets (e.g., Tindale 1928), are now classified with the short-horned grasshoppers (suborder Caelifera) and form the family Cylindrachetidae within the superfamily Tridactyloidea (Rentz 1996). Included with them in this superfamily are the Tridactylidae ('pygmy mole crickets') and Ripipterygidae ('mud crickets') (Günther 1994; Flook *et al.* 1999). All cylindrachetids are burrowing insects, highly modified for a subterranean existence. The body shape is cylindrical, the fore legs are highly modified for digging, the reduced mid and hind legs recess into the sides of the abdomen, simple eyes replace the compound eyes, antennae and cerci are reduced, and wings are entirely absent (Figures 1–3). Of all the orthopteroid insects, they are considered to be the most strongly modified morphologically for a subterranean life (Kevan 1989).

In the most recent revision of the family (Günther 1992), three genera and 16 species were recognized. Fourteen species are Australian, one is Argentinean and one putatively occurs in New Guinea. Günther erected a new genus, *Cylindraustralia*, to contain 13 of the Australian species. Prior to his revision, all known Australian species were placed in *Cylindracheta* Kirby, a genus Günther restricted to one species from the 'Top End' of the Northern Territory. *Cylindraustralia* species occur widely across the Australian continent but are absent from the south-eastern portion.

Although the taxonomy of cylindrachetids has been reasonably well studied, their biology has received scant attention (Barrett 1928; Tindale 1928; Richards 1980; Günther 1992; Rentz 1996). Some published information is misleading or incorrect and nothing has been recorded hitherto of the eggs and early immature stages. Of course, living almost wholly subterranean lives, the insects are rarely observed and make difficult subjects for study.

In Western Australia, sandgropers have gained a reputation as agricultural pests, being reported to damage wheat, barley, oats, sweet lupins and



Figures 1–5 *Cylindraustralia kochii*. (1–2) Adult female and male, respectively (note bands of pigmentation around abdomen, in male interrupted dorsally on segments 7–9). (3) Last stage nymph (note absence of abdominal pigmentation; dark 'marks' along dorsal median line are gaps in underlying fat body visible through transparent integument). (4–5) Surface trails produced by adults burrowing just beneath surface of ground: (4) simple trails in natural bushland; (5) branched trails on compacted sand surface of farm road.

tagasaste between Perth and Geraldton (Richards 1980; Rentz 1996; Wiley 2000). Only anecdotal and circumstantial evidence, though, was produced by these authors to show that sandgropers were the cause of the observed plant damage.

While the insects themselves are rarely encountered, their characteristic trails (Figure 4) are a common sight on bare sandy ground in Western Australia. Two species (*C. kochii* (Saussure) (syn. *psammophila* (Tindale)) and *C. tindalei* Günther) are known to be extant in and around Perth.

The present study was undertaken in an attempt to elucidate the life histories, behaviour and ecology of sandgropers.

MATERIALS AND METHODS

Over 900 spirit-preserved specimens of *Cylindraustralia* in the collection of the Western Australian Museum were examined in this study. Most were collected by the author from 2002–2005, the remainder being donated by members of the

farming community and the general public in response to a media appeal. By far the bulk of the material studied was comprised of *C. kochii* while most of the remainder consisted of *C. tindalei*.

Although sandgropers have occasionally been found in pitfall traps, the author's deployment of gutter traps and pitfall traps combined with drift fences at a number of sites failed to yield specimens. Following on foot close behind farm ploughs turning over soil under pasture yielded many specimens. Others were obtained from near-surface galleries: by driving back and forth along sandy roads and firebreaks on the margins of bushland shortly after rain, it was possible to recognize fresh trails where they crossed the vehicle's tyre tracks (Figure 5). Most specimens obtained for this study, however, were turned up by digging with a spade beneath pastures and weeds on farms.

Study sites where significant work was undertaken are as follows (short-hand names used in this paper appear in quotation marks): "Dandaragan site"– Annamullah Farm, 6 km NNE of Dandaragan, 30°38'S, 115°45'E; "Horrocks site" – Willi Gulli North Farm, 18 km W of Northampton (2 km E of Horrocks), 28°22'S, 114°27'E; "Eurardy site" – Eurardy Station, 89 km N of Northampton, 27°34'S, 114°40'E; M. and D. Webb's farm, 23 km E of Northampton, 28°18'52"S, 114°51'58"E; and "Great Sandy Desert", various sites approximately 220–280 km SE of Broome, between 19°04'13"S, 123°44'05"E, and 19°17'52"S, 124°26'27"E.

Various methods of killing and preserving specimens were trialled. For the purposes of later dissection, best results were obtained by freezing specimens. Where this was impractical, freshly killed specimens were injected with and stored in 10% formalin (although injection caused the abdomen to inflate and extend). Several specimens were killed by spraying the head and thorax with electrician's freezer and were then immediately dissected in saline to check for living parasites or commensals in the gut, abdominal cavity and genital tracts.

Live specimens were maintained in containers of moist sand or sandy loam with various plants: Cape Weed (*Arctotheca calendula*), Wild Oats (*Avena fatua*), and seedlings germinated from commercial 'mixed budgie seed'. Glass-bottomed and clear plastic containers permitted observations of burrowing activity. Eggs were reared on tissue wads in glass vials in humid boxes. The boxes were kept at room temperature (18–30°C) and open vials of saturated salt solution provided moderate humidity.

Specimens were identified by comparison with specimens in the Western Australian Museum determined by Dr Kurt Günther and by means of Dr Günther's 1992 revision of the family Cylindrachetidae. Some specimens from the Horrocks and Great Sandy Desert sites could not be matched to any of Günther's taxa and appear to represent undescribed species referred to below as 'Species A' and 'Species B', respectively.

The pronotal width of all specimens was measured to determine the number of instars. The pronotum is a rigid structure that is easily and reliably measured across its greatest width.

Population sampling at the Dandaragan site was undertaken approximately every second month although the October sample was not in sequence with the rest. The method used was to excavate a large pit at least 1 x 2 m in area and 1–2 m deep using a spade and trowel and to collect every specimen encountered as the soil was turned over. Excavation required 2–4 days.

OBSERVATIONS AND DISCUSSION

Life Stages and Morphology

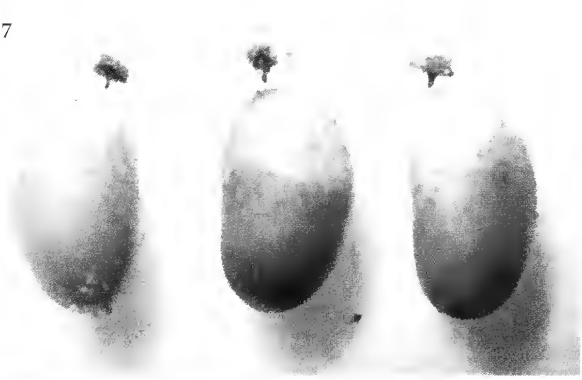
Adults

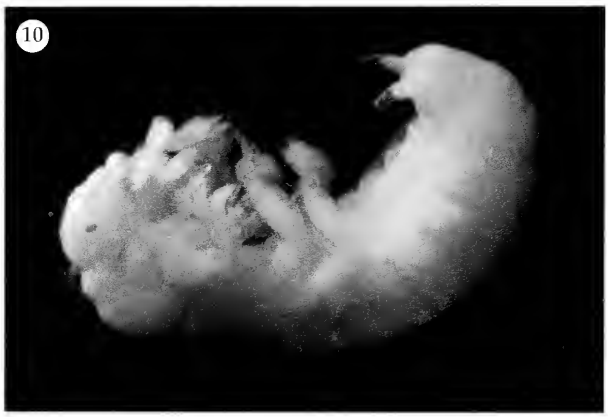
Apart from having completely developed genitalia, adults are distinguishable from nymphs in having the abdominal integument wholly or largely tan-coloured (Figures 1, 2) (in males of *C. kochii* the tan pigmentation is usually broken by narrow, colourless, intersegmental bands). The abdominal integument of all nymphal stages, by contrast, is completely colourless and, being transparent, the abdomen appears white or cream because of the underlying fat body (Figures 3, 11).

Males and females are similar in size. Among a sample of *C. kochii* adults from the Dandaragan site, pronotal widths of males ranged from 6.75–8.20 mm (mean 7.35 ± 0.33, n = 20) and of females from 6.80–8.30 mm (mean 7.4 ± 0.44, n = 14). The sexes are also very similar morphologically but can be distinguished by the external genitalia. As Günther (1992) noted, males possess a pair of short, stout spines on the paraprocts near the insertions of the cerci (Figure 13). Females lack these spines and, instead, possess a pair of rudimentary gonovalves, the tips of which sometimes protrude slightly beyond the apical margin of the 8th abdominal sternite (S8, Figure 12). In *C. kochii* (but not other species), adult males are further distinguished by a large unpigmented patch on the dorsal side of abdominal segments 7–9 (Figure 2).

Eggs

Eggs were first observed in the oviducts of dissected females of *C. kochii*. These oviducal eggs were elongate-ovoidal, *c.* 7.0 mm long and 3.3 mm in diameter, flat to slightly concave on one side (thus being bilaterally symmetrical), and had a tiny appendage *c.* 0.5 mm long anteriorly (Figure 6). The chorion was smooth, unsculptured and translucent





Figures 6–11 *Cylindraustralia kochii*. (6) mature eggs dissected from oviduct (for detail of apical appendages, see Figures 21–23); (7) laid eggs showing attachment pedicels and adhesive disks with adherent sand grains (collected in October, chorions dull and opaque); (8) vertical section of earth showing two freshly laid eggs suspended in their chambers (upper egg has a drop of ground water on right side and a fungus grows on chamber floor); (9) freshly laid egg with red chorion; (10) larva shortly after eclosion (for more details see Figures 24-26); (11) newly emerged first instar nymph with its eggshell.

off-white. The appendage consisted of a doughnut-shaped mass of gelatinous material about 0.7 mm in diameter attached to a central disc which was in turn connected axially to the egg by a short flexible stalk or pedicel (Figures 21–23). At 400x magnification the gelatinous mass was observed to consist of tightly packed bundles of fibrils with their free ends outermost. This appendage later proved to be a device for attachment of the egg to the substrate.

Laid eggs of *C. kochii* were first observed *in situ* at the Dandaragan site in May 2003 when over 40 were uncovered, each enclosed in a small chamber (Figure 8). The eggs were suspended from the ceilings of their chambers on short flexible pedicels, the upper ends of which expanded into rounded discs (Figures 7, 24). The discs were firmly cemented to the soil by some substance that proved to be water-insoluble. Otherwise, the eggs were free of contact with the soil. Most eggs in this lot were translucent white (like oviducal eggs) and presumably freshly laid. A few were wholly dark red (Figure 9) while others were white variously mottled with pink. The red/pink pigmentation was confined to the chorion and, in the wholly red individuals, to the stalk and disc as well but never extended to the yolk which was completely colourless. Many eggs, too, bore a drop of clear liquid on one side (Figure 8) – evidently ground water that had trickled down from the chamber ceilings. At the same site in October 2004, 32 eggs were excavated. The majority were wholly or partly pink and only six were pure white but, in all cases, the chorion was dull and opaque.

No laid or oviducal eggs were found for *C. tindalei* but one near-mature egg (4.3 mm long) in an ovariole had a gelationous appendage much like that of oviducal eggs of *C. kochii*. Oviducal eggs of Species B, however, lacked a pedicel and attachment disc. Instead, each egg had a flat apical cap of gelatinous material (*ca.* 0.8 mm diameter) directly and broadly attached to the chorion.

The glueing of eggs to the substrate, and particularly their suspension on pedicels, is something not reported for other tridactyloid families. Eggs of Tridactylidae and Ripipterygidae, lack any sort of appendage as far as currently known. Eggs of one tridactylid have been reported to be laid in batches of 10–20 in the ends of galleries (Urquhart 1973, cited by Günther 1994) while those of ripipterygids are laid singly in excavations made with the gonovalves much as in the manner of acridids (Schremmer 1972; Gambardella 1971; both cited by Günther 1994).

Larva

In the laboratory, eggs eclosed to a pre-nymphal stage or 'larva' (Figures 10, 25–27), the equivalent of the 'vermiform larva' of the Acrididae (Uvarov 1966). The larva was a setose individual of distinctive form enveloped in a thin, transparent membrane (the 'provisional cuticle' of Uvarov). This membrane, unlike that of acridids, lacked setae and spicules but on the median line of the frons had a thin, brownish, sclerotized and slightly serrated carina (Figures 26, 27), presumably an egg-burster. Other characteristics were: fore legs reflexed backwards against body; prothorax much wider than long and slightly biconvex (weakly depressed medianly); and mesothorax not encapsulating hind part of prothorax. This stage is short-lived, the provisional cuticle being shed almost immediately after eclosion from the egg, or at least within a couple of hours, giving rise to the first nymphal instar.

Nymphs

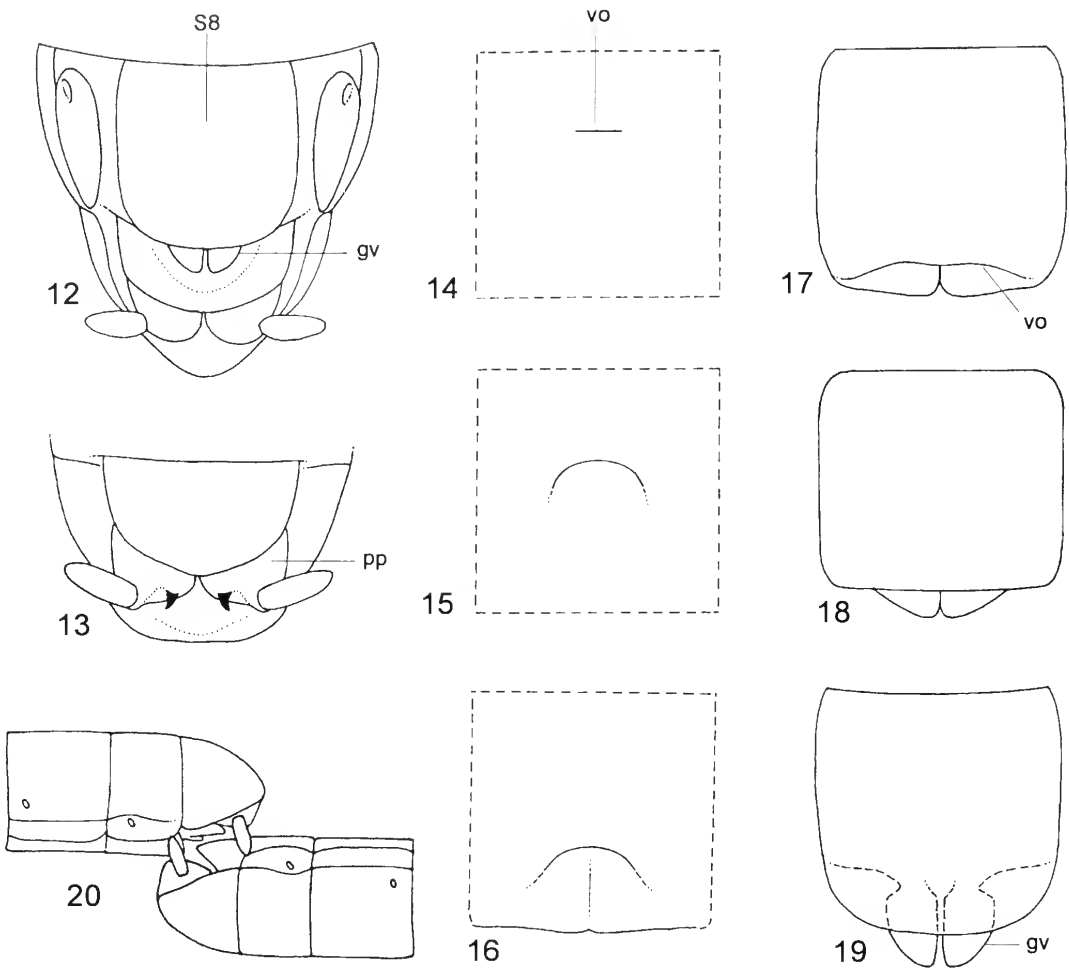
An individual of typical sandgroper form with the fore legs directed anteriorly emerged from the larval skin (Figure 11). In keeping with convention (David Ragge, pers. comm.), this stage should be regarded as the first nymphal instar. It is at first wholly white with pink eyes but gradually (over a period of days) develops tan colouration in the head and thorax as the cuticle hardens and the eyes turn black. These changes occur before the nymph leaves the egg chamber.

Nymphs are much like adults and are comparatively uniform morphologically. However, the development of the external genitalia provides some characters enabling determination of the sex of an individual and (in females) the particular instar to which it belongs. Tentative determination of the number of nymphal instars in *C. kochii* was made possible by measurement of a large number of nymphs of various sizes and the hatching of early stages from eggs in the laboratory.

The size-frequency distribution for all *C. kochii* collected from the Dandaragan site (Figure 28) reveals four peaks suggesting the existence of four nymphal instars. However, as the larger size classes were poorly represented, the histogram may not present an accurate picture. If the relative increase in pronotal width from instar to instar was constant in keeping with Dyar's 'law' (CSIRO 1991), one would expect another peak to occur around the 5.0 mm mark.

Anatomical evidence for the existence of five nymphal instars was found on the eighth abdominal sternite (S8) of females: the vaginal opening is evident from the first instar, and increases in size and shifts rearward with each moult; in later instars, the gonovalves form from the hind margin of S8 (Figures 14–18).

Male nymphs can be recognized by the absence of the vaginal groove and/or developing gonovalves. Additionally, from about the 3rd instar, they possess developing paraproct spines. These are at first



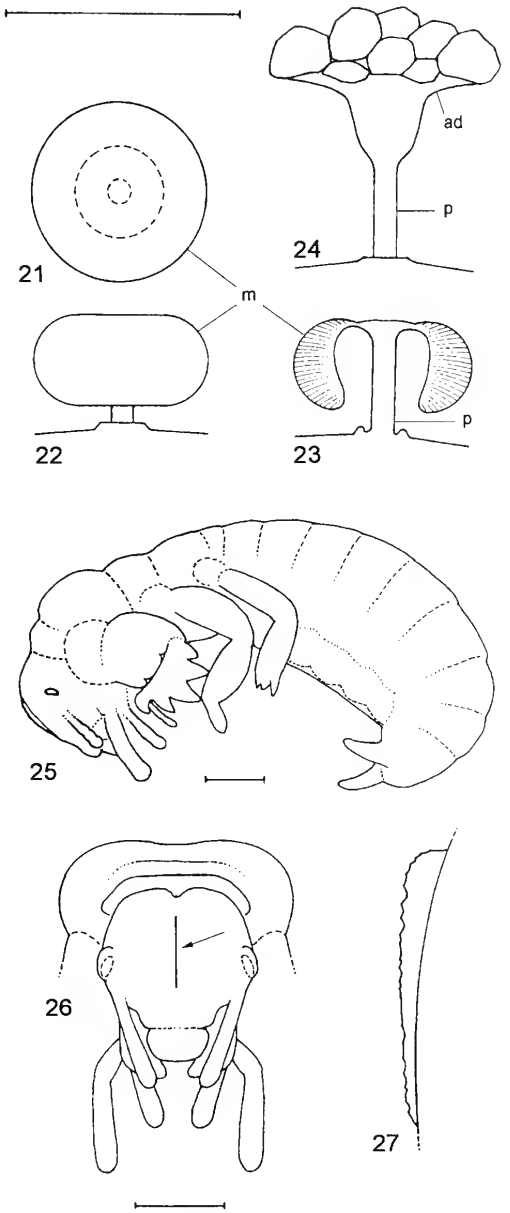
Figures 12–20 Sketches of genital areas of *Cylindraustralia kochii* (not to same scale): (12) underside of apex of abdomen of adult female, somewhat inflated to show various sclerites and apices of gonovalves (normally hidden behind 8th sternite); (13) same of adult male, showing copulatory spines (solid black) on paraprocts (pp); (14–18) eighth sternite of 1st–5th female nymphal instars, respectively, showing development of vaginal opening and gonovalves (abdominal sclerites of early instars are unsclerotized and ill-defined, thus approximate boundaries of S8 are indicated by broken lines); (19) eighth sternite of adult female showing outline of gonovalves; (20) presumed juxtaposition of hind ends of male and female during copulation (only with this arrangement could copulatory spines of male engage hind edge of S8 of female, pulling it down and permitting intromission of genital armature into vagina). Abbreviations: gv, gonovalves; pp, paraprocts; S8, eighth sternite; vo, vaginal opening.

almost imperceptible, colourless tubercles but, in later instars, they become more pronounced and more acute and, in the final nymphal instar, acquire pigmentation and are strongly sclerotized (*cf.* Figure 13).

Putative stridulatory organ

A putative stridulatory apparatus on the mouthparts of cylindrachetids was described and figured by Günther (1992) and Rentz (1996). It consists of a field of microscopic tubercles arranged in rows on the ventral surface of each mandible and a single row of about seven short ridges on the opposing dorsal surface of the basal segment of each maxillary palpus. Günther noted this apparatus in both sexes. It is now clear that it occurs in all nymphal instars as well. Thus, it is unlikely that the apparatus plays a part in mate-attraction, if in fact it produces sound at all. I detected no stridulatory sounds from sandgropers, even when holding them close to my ear.

Lawrence and Britton (1994, pl. 2) described and



Figures 21–27 *Cylindraustralia kochii*. (21–24) Sketches of apical appendage of egg: (21) prior to laying, top (axial) view; (22) same, lateral view; (23) same, sectional view; (24) after oviposition (everted adhesive disk is cemented to sand grains in ceiling of egg chamber, its outer edges being poorly defined). Abbreviations: ad, adhesive disk; m, mucilaginous ring; p, flexible pedicel. (25–27) Sketches of larva: (25) lateral view (note reflexed fore leg); (26) anterior view of head and prothorax showing location of frontal carina (= egg-burster, arrowed); (27) frontal carina in left lateral view, not to scale. Scale lines, 1 mm.

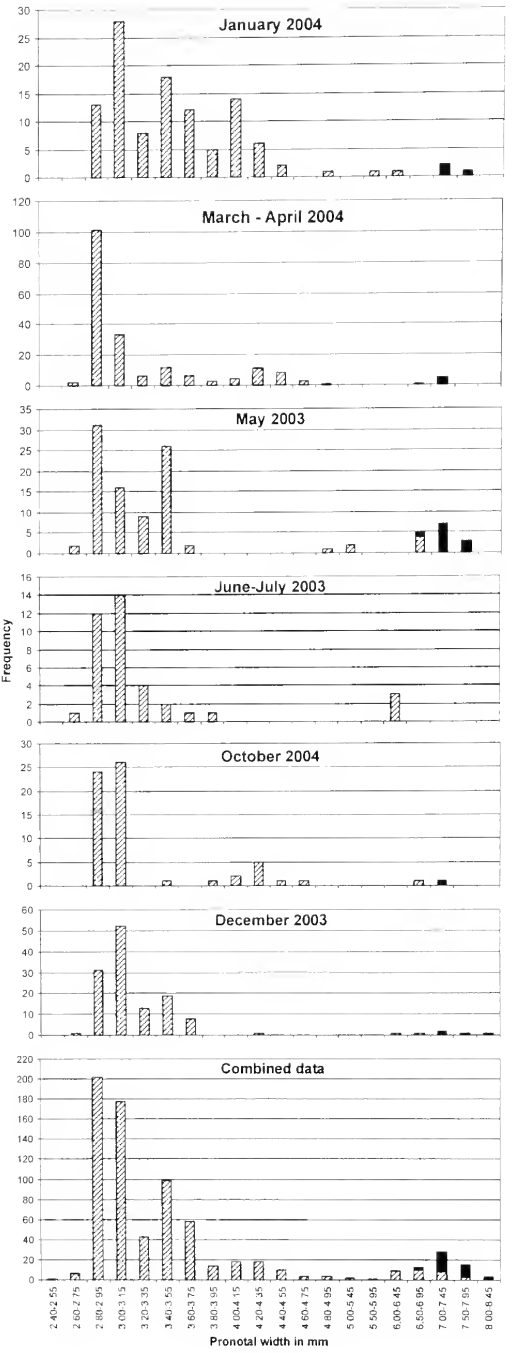


Figure 28 Frequencies of various size classes (based on pronotal width) of nymphs (hatched) and adults (solid black) of *Cylindraustralia kochii* collected in different months at the Dandaragan study site. The combined data set is based on specimens from the six seasonal samples plus some additional ones. Note that above a pronotal width of 5.00 mm, size class intervals increase from 0.2 to 0.5 mm.

figured similar patches of minute tubercles (termed 'asperities') on the dorsal surfaces of the mandibles of certain pyrochroid and cucujid beetle larvae but did not attribute any function to them.

Odour glands

Live specimens of *C. kochii* (and other species) often emitted a strong, slightly pungent odour when handled. Günther (1992) noted a number of integumental glands and gland openings in cylindrachetids although he did not discuss their functions. They included a gland opening on the inside of each fore femur, glandular tissue in each mid and hind tibia, a gland opening in each laterosternite of the 3rd abdominal segment and, in males of *C. kochii*, an area of glandular tissue beneath abdominal tergites 7–9. In order to determine the origin of the odour, each of the gland areas of a freshly killed adult of *C. kochii* was excised in turn, crushed between the fingers and the residue sniffed to check for odour. Only the 3rd abdominal segment produced a very strong and lasting odour identical to that noticed in handling live specimens.

Dissection revealed a gland sac attached to each of the two gland openings on the 3rd abdominal segment. These sacs are evidently reservoirs for the gland secretion. An apodeme adjacent to each gland opening provides attachment for a muscle (possibly serving to open or close a valve). The gland openings and sacs were found in adults of both sexes and all nymphal instars. Consequently, the gland secretion is unlikely to play a role in mate attraction and a defensive function seems more likely.

Ecology and Behaviour

Habitat

Field observations, reinforced by museum collection data, reveal that sandgropers inhabit a wide variety of sandy soils including calcareous and siliceous sands and sandy loams. *C. kochii* inhabits diverse habitat types including coastal dunes, sand plains with heath ('kwongan') or shrubland vegetation, red desert dunes with tussock grasses (principally *Triodia* spp.), red sandy loams with open eucalypt woodland and comparatively hard sandy loams with *Acacia* shrubland in the Gascoyne of WA.

Hundreds of specimens of *C. kochii* were collected from agricultural land beneath pastures of mixed weeds including Cape Weed, lupins, clover and exotic grasses or beneath young cereal crops (wheat and barley). Some of this land had been cleared for several decades and the nearest remnants of native vegetation were tens of kilometres away. A smaller number of specimens of *C. kochii* and *C. tindalei* were collected from suburban gardens beneath exotic plants or patches of weeds. Clearly these sandgropers are not dependent on native flora.

Burrowing

Observation of specimens in moist sand in glass-bottomed and clear-sided containers revealed that they create galleries by parting the soil ahead of them with synchronous lateral motions of their fore legs, compressing it to the sides. They do not loosen soil and shift it behind them the way many other burrowing insects do. After each stroke of the fore legs, the insects shuffle forwards on the mid and hind legs. Upward motions of the head, observed in hand-held specimens, may also help compact the walls of the galleries. By twisting the fore body as they progress, the insects are able to compact the soil up and down as well as sideways. The galleries so-formed are smooth-walled, cylindrical and only marginally wider than the insects creating them. Sandgropers move easily and quickly both forwards and backwards within their galleries. Only the mid and hind legs are involved in walking, the fore legs being held stiffly forwards off the substrate.

At the Dandaragan site, adults and large nymphs of *C. kochii* were frequently excavated from depths of 1.0–1.8 m (and given the presence of eggs at 1.9 m, adult females must at times have burrowed to this depth). They could not have gone much deeper because of a gravel layer at 2 m. Smaller nymphs were also found in numbers at depths of 1.5 m or more, although many (if not all) of them would have hatched there. The soil at depths of 40 cm and deeper was very compact and could be cut in blocks. It is testimony to the strength of sandgropers' fore legs that they are able to force a passage through such a compact medium.

Specimens were usually found in horizontal to somewhat inclined burrows, rarely in vertical galleries. In some cases they had found their way into large earthworm shafts which abounded at the Dandaragan site. The galleries of several nymphs and adults that were traced carefully wound erratically downwards, having horizontal, inclined and vertical sections. Several adults and late stage nymphs were encountered at the ends of galleries facing away from the blind ends. How these individuals could have executed turns, allowing them to reverse into these galleries, remains unexplained.

During summer excavations at the Dandaragan site, no live sandgropers were found in the top 20 cm of the soil (the A horizon) which was dry and hard. All specimens occurred in the moist subsoil. The A horizon, however, was almost honeycombed in places with large galleries created on previous occasions. In winter, too, no sandgropers were found in surface soil that had become dry. They ventured into the surface zone only when it was damp following recent rain.

A common habit of sandgropers is to burrow long distances just beneath the surface of the soil producing raised ridges or 'trails' on the surface (Figures 4, 5). Adults of *C. kochii* burrow 1–2 cm beneath the surface, smaller nymphs at comparatively shallower depths. Beneath each raised trail (and scores were examined) was a gallery. The longest continuous section of trail observed was 10 m but the insects may travel much further than this. Trails can persist for weeks or even months and often criss-cross the ground.

In southern Western Australia which has a Mediterranean climate, several sandgroper species produce trails only during the cooler, wet months of the year from about April or May to September or October and only for 1–2 days after soaking rain while the surface soil is moist. Fresh trails appeared throughout the day but not at night. Heavy showers also elicited trail-forming by Species B at the Great Sandy Desert sites in July 2005. Typically, this tropical area has dry winters, receiving its rainfall during the summer monsoon season.

It was sometimes found that sandgropers had backed up one or more metres from the blind (leading) ends of their near-surface galleries. Also, many trails and their underlying galleries branched, especially those occurring on compacted surfaces such as dirt roads (Figure 5). Evidently, when the insects encounter an obstacle, such as soil that is too hard to penetrate, they back up and strike off in a different direction.

Counts of the stages and sexes of sandgropers collected while trail-forming are shown in Table 1. For *C. kochii*, the behaviour seems to involve mainly adult males (92% of specimens), suggesting it could be associated with mate-seeking. A similar but less pronounced trend is noted for *C. tindalei* (72% of specimens). By contrast, both sexes were almost equally represented for Species B. Larger samples will be required to determine if there are persistent species differences here. Given that nymphs as well as adults engage in trail-forming, this behaviour may represent a general dispersal mechanism. By burrowing close to the soil surface which yields, sandgropers would be able to progress faster and with less effort compared with burrowing at greater depth and still maintain cover.

Soil moisture is clearly important to the burrowing activities of sandgropers. First, it softens the soil (sandy loams often become mortar hard when dry). Second, it binds sand grains ensuring that galleries remain open behind the insects, providing them with a ready means of retreat.

Table 1 Numbers of specimens of sandgropers collected while trail-forming (i.e., burrowing just beneath the surface of the soil causing a raised ridge). The species *C. arenivaga* (Tindale) was observed by the author in the Gibson Desert in 1982.

Species	adult males	adult females	nymphs
C. arenivaga	2		
C. kochii	22	1	1
C. tindalei	13	4	1
C. tindalei?			1
C. tindalei x *kochii* (?)	1		
Species B	8	7	4

Egg chambers

Egg chambers (Figure 8) measured *c.* 20 mm in length, were smooth and evenly concave at one end and rough at the other. They appeared to have been formed from the blind ends of horizontal or slightly inclined galleries through back-filling of the access burrows following oviposition.

While egg chambers were clearly separate, they were often loosely aggregated. For example, at the Dandaragan site, one group of 19 chambers occurred within a block of soil measuring *c.* 30 x 20 x 20 cm. Within this group there were tighter clusters of 2–5 chambers, the chambers being separated by as little as 1–2 cm. Egg chambers were found at depths of from 40–190 cm.

The process of egg chamber formation and oviposition was not observed but must involve the female in some special manoeuvres including at least two reversals of direction. As a female creates a blind horizontal gallery, the end of which will become the egg chamber, she would face into the blind end. To oviposit in this blind end, she would need to reverse direction and, to attach her egg to the ceiling, must lie on her back. As the egg is extruded from the vagina, the adhesive disc on its anterior (leading) end would contact the ceiling and cement the egg in place. The female must then withdraw and reverse direction again in order to attend to closure of the brood chamber (females having no strongly sclerotized structures at their hind ends that could serve to scrape or push soil). It would be impossible for a female to reverse direction in the narrow confines of a typical gallery, yet I observed nothing that could have served as a 'turning chamber'. However, I did encounter some widened sections of gallery (about twice as wide as usual) which could have been the source of soil used for back-filling access burrows.

Population density and distribution

Other than finding specimens in near-surface galleries following rain, attempts to find sandgropers in bushland areas by means of digging were unsuccessful, even though many holes were dug in areas where trails were common. This would suggest that either the insects were sparsely distributed or they were deeper than my excavations (usually not deeper than 50 cm).

At the Dandaragan site, however, a very different situation prevailed. In mid May 2003 when initial observations were made by the author, a 1 x 1 m hole dug almost anywhere in a paddock carrying only pasture produced one or more specimens. For example, one exploratory excavation about 1m x 1m x 80 cm deep yielded 11 small nymphs. About 50 m distant, an excavation 1 m x 1 m x 30 cm deep yielded five adult males but no nymphs.

The greatest density was recorded at the same site during excavation in late March/early April 2004 when the largest and deepest pit was dug (3 m x 1 m x 1.8 m [in part]). Calculations produced a figure of *c.* 100 specimens for each square metre of surface. Specimens were absent from the dry A horizon (c. 20 cm deep) but were numerous at all depths of the moist B horizon down to 180 cm. The greatest density occurred in the 60–90 cm deep zone (101 specimens/m^3) and the 160–180 cm deep zone (100 specimens/m^3). The size/frequency distribution of this sample is represented in Figure 28.

At the Horrocks site in August 2003, the author excavated seventeen 1m x 1m pits to a depth of at least 40 cm at various locations around the farm to check for the presence of sandgropers. All were in deep yellow sand under pasture. In one paddock, only *C. kochii* was found. In an adjoining paddock, mainly Species A was found with an occasional *C. kochii*. There was very little observable difference between these two paddocks in terms of soil and pasture cover. Several excavations in a paddock situated in a vale produced no specimens at all. Clearly, the distribution of sandgropers is patchy in seemingly suitable habitat, but what factors determine the presence or absence of these insects has yet to be determined.

Food and feeding

Examination of the gut contents of 62 winter-collected and 100 summer-collected specimens of *C. kochii* and *C. tindalei* revealed that they had consumed a diversity of materials, most of it being of vascular plant origin although insect and arachnid remains were also identified in many specimens. Fungal tissues, including hyphae, sporangia and spores, were present more often than not, but mostly in small quantities. Sand grains, too, were almost always present throughout the intestine but, comprising only a minor component of gut contents, were probably accidentally ingested with the food. The food was well masticated and finely divided, so identification sometimes required comparison of tissues at the cellular level under a compound microscope.

Sloughed peritrophic membranes were always present in the gut and enclosed the food, regardless of the quantity of the latter.

Ingested plant material consisted mainly of underground parts (roots and stolons) but also comprised aerial parts such as stems and leaves of grasses (including cooch, wheat and barley), dicotyledonous leaves (e.g., Cape Weed), floral bracteoles of Asteraceae, and seeds of several kinds. Most seed tissue was not identified but several specimens of *C. kochii* from the Horrocks and Dandaragan sites had eaten seeds of 'double-gee' (*Emex australis*), a pest weed in these areas. Double-gee seeds are contained in hard, spined fruits which the insects evidently chew open.

Plant material varied from fresh (e.g., white rootlet or chlorophyll-containing leaf tissue) to old and partly decomposed (brownish tissue containing lots of fungal hyphae and spores). The presence of chlorophyll-containing leaf tissue matching that of wheat leaves in the intestines of sandgropers collected from wheat fields could be taken as convincing evidence that the insects damage wheat as reported by Richards (1980). There is some possibility, though, that sandgropers may simply be availing themselves of stems and leaves pulled into the soil by cutworms (noctuid moth larvae) rather than being primary pests. On a farm east of Northampton, the author examined a patch of barley crop purportedly thinned by sandgropers. Numerous young barley plants had turned yellow and many loose stems and leaves were found partly pulled into the soil. Excavation around these damaged plants yielded not sandgropers but numerous pink cutworm larvae (*Agrotis munda* Walker). These cutworms are reported to cause the kind of damage observed (Common 1990).

Fungal tissue in gut samples consisted mostly of rusts, saprophytic and mycorrizal fungi probably ingested with root, stem and leaf tissue. In a few samples, though, significant amounts of fungal tissue suggested direct browsing, one such sample containing VAM (vesicular-arbuscular mycorrhiza) spores (Dr Neale Bougher, pers. comm.).

A variety of invertebrates were identified among gut contents (Table 2). In most cases, the remains of only one or two insects were present. However, two adults of *C. tindalei* had consumed numerous worker termites, clearly demonstrating purposeful predation rather than accidental ingestion. Most of the listed invertebrates are likely soil inhabitants, even the native bee. Six or more insect egg chorions about 4 mm long and possibly from acridid grasshopper eggs were found in the gut of one adult male of *C. kochii*.

Cannibalism was encountered in the very dense population of *C. kochii* at the Dandaragan site among summer-collected specimens (see Table 2). Second and older instar nymphs and adults had consumed first instar nymphs which formed the bulk of the population at the time. In several individuals, the gut contents included fragments of both the front and hind ends of the prey, providing

Table 2 List of arthropod food items identified among the gut contents of *Cylindraustralia kochii* and *C. tindalei* and the numbers of specimens in which they were found.

Food item	*C. kochii*	*C. tindalei*
Dermaptera	1	
Isoptera – workers	2	4
?Orthoptera: ?Acrididae – eggs	1	
Orthoptera: Cylindrachetidae – nymphs	17	
Hemiptera: Fulgoroidea		1
Diptera: Mycetophilidae – larva		1
Diptera: Sciaridae – adult		1
Diptera: Sciaridae – larva	1	
Diptera: Cylcorrapha – larva (1st instar?)		1
Lepidoptera: Noctuidae, *Agrotis* – larva	1	
Lepidoptera: unidentified larva	3	
Coleoptera: Scarabaeidae, Melolonthinae – adult	3	1
Hymenoptera: Formicidae – worker	10	2
Hymenoptera: Colletidae, *Dermatohesma* – adult	1	
Araneae		1
Acarina	2	3
unidentified chitinous remains	7	

convincing evidence of predation as opposed to accidental ingestion.

Evidence that first instar nymphs consume some or all of their eggshells was found in 11 specimens collected at Dandaragan in January and March/April. Among the gut contents were fragments of fenestrated membrane (consistent with the outer layer of sandgroper egg chorion) plus large numbers of colourless, refractive, spherules (diameter *ca.* 0.01 mm). Similar spherules occur in clusters in the inner layer of the egg chorion. Further evidence was obtained when four newly hatched first instar nymphs were maintained in glass vials with their eggshells. Torn edges of the chorions, at first entire, became distinctly serrated and eroded due to the feeding activity of the nymphs.

When first instar nymphs leave their egg chambers deep in the soil, their most likely food source would be the very fine roots found to lace the soil there.

In terms of gut contents, there were some notable differences between specimens collected in 'winter' (May to September; see Table 3) and those collected in 'summer' (December to April; see Table 4): 93% of winter specimens had eaten plant material compared with only 13% of summer specimens. Only 44% of summer specimens showed evidence of recent feeding and 57% of those had eaten an insect (in 18 of 25 cases, another sandgroper). The

Table 3 Summary of gut contents of sandgroper specimens collected during 'winter' months (i.e. late April to September) from various localities in south-western Australia.

Species	No. of specimens examined	Numbers of specimens that had eaten certain items		
		Plant material	Seed material	insect/mite
C. kochii	45	42	24	12+
C. tindalei	17	11	3	10

Table 4 Summary of gut contents of specimens of *Cylindraustralia kochii* collected in 'summer' months (i.e., December to early April) from the Dandaragan site. Cannibalism is represented in the column headed 'Sandgroper'. The column headed 'Egg chorion' refers to first instars that appear to have consumed their own egg chorion after hatching. For an explanation of the right-hand column, see under *Predators, Parasites and Associated Organisms – Amoebae.*

Sample	n	Numbers of specimens that had eaten certain items					
		Any food	Plant matter	Sand groper	Other insects	Egg chorion	Number with amoebae and/or rectal convolutions
Early Dec.	40	6	6	1	2	3?	28
Late January	30	20	5	13	2	2	22
March/April	30	18	2	4	3	9	10
Combined	100	44	13	18	7	14	60

low incidence of plant-feeding during summer might suggest that the insects avoid the dry surface layers of the soil where most of the grass and herb roots occur. In summer, too, cooch grass was the only live plant at the study site. Yet, among the plant material consumed by some summer-collected specimens were grass-leaf and seed tissues. Their presence in specimens collected at depths of 60–95 cm suggests that those individuals had recently ventured to or near the surface to feed.

The occurrence of amoebae in the gut of summer-collected specimens and the seemingly associated condition referred to here as 'rectal convolutions' is discussed in detail below under *Predators, Parasites and Associated Organisms*.

Faecal pellets observed in the rectum, were usually solid, roughly cylindrical, and enclosed in peritrophic membrane.

The gut contents of two adult females of Species B consisted mostly of various plant tissues along with small amounts of arthropod chitin. Günther (1992) and Tindale (1928) recorded plant tissue and insect chitin in the alimentary tracts of a further three species of *Cylindraustralia*, so omnivory is clearly widespread in the genus.

Annual Life Cycle and Development

Adults and nymphs of a broad range of sizes were present in population samples of *C. kochii* collected throughout the year (Figure 28). From the histograms it will be seen that the first and second nymphal instars were by far the most numerous stages present in each sample. The third and fourth instars, by contrast, were very poorly represented, being scarcer even than the fifth instar. As revealed by Table 5, laid eggs were found in the soil at intervals throughout most of the year. The occurrence of eggs and early instars through most months of the year initially suggested the possibility of year-round breeding in *C. kochii*. This possibility, however, is not supported by other observations.

Dissection of adult females collected from May to August revealed that most carried eggs ready to lay in the oviducts or at least had near-mature ova in the ovaries. For example, five adult females ploughed up on 10 May 2003 all carried eggs ready to lay. By contrast, the ovarioles of the only four females collected in summer (late January and late March) had no ova near egg-size. Instead, each ovariole contained only a series of very small to minute ova. Additionally, the spermathecae of all four females were devoid of sperm. Thus it is likely that these females were very young, pre-reproductive individuals.

At the Dandaragan site, freshly laid (translucent) eggs were found only during the late May and June–July visits. All eggs found later than July through to December were opaque and showed no signs of embryological development. Developed and hatching eggs were only found in January.

Several apparently freshly laid eggs collected in June/July were maintained in the laboratory for several weeks during which time they turned opaque and some succumbed to mould but none hatched. A few were opened to check for signs of embryological development but none was found.

In January 2004, a number of opaque eggs were excavated, some showing signs of development (eye spots and legs vaguely visible through the chorion). On this same occasion, empty egg-shells were found along with tiny, clearly newly emerged nymphs in several chambers. A number of eggs hatched over subsequent days. During a March–April excavation at the same site, only one (opaque) egg was found.

In October 2004, 32 opaque eggs were excavated at Dandaragan and returned to the laboratory. Although a few succumbed to mould attack, turned black and/or shrivelled, most eggs remained outwardly unchanged until late February 2005. Four eggs hatched between 24 February and 1 March 2005 and several more probably would have hatched had they not been dissected to check for embryological development. The first such dissections were on 17 January: two eggs contained small embryos and another a live, almost fully developed larva. On 3 February, a number of eggs were wet with distilled water to varying degrees and over varying periods from one day to two weeks to see if this might induce eclosion. However, these treatments were ineffectual. Eleven

Table 5 Dates when eggs of *Cylindraustralia kochii* were excavated from soil.

Month (days), year	Location	Comments
January (28-31), 2004	Dandaragan	Many, opaque, with embryos or hatching
March (29)-April (1), 2004	Dandaragan	One, opaque
May (28-30), 2003	Dandaragan	Many, translucent
June (30) – July (2), 2003	Dandaragan	Many, translucent
August (20-26), 2003	Horrocks	Two
October (27-29), 2004	Dandaragan	Many, opaque
November (16), 2002	Mullaloo (Perth)	Two, opaque
December (3-6) 2003	Dandaragan	A few, opaque

eggs remaining unhatched on 14 March were dissected and, while life had expired in all of them, embryological development had proceeded to varying stages in several and two contained fully formed larvae.

Four first instar nymphs reared from eggs in late February/early March 2005 were maintained alive in moist soil with germinating mixed budgie seed. They thrived (as evidenced by their increasingly large abdomens) but succumbed to disease one by one, the last surviving for seven months. None moulted to the second instar.

Taking account of the above data, it seems likely that oviposition occurs from May to August; the egg chorion is shiny and translucent at first but gradually turns dull and opaque; eggs remain dormant until mid-summer when they develop and hatch. If it is the norm that hatching is restricted to mid-summer, then the year round presence of first instar nymphs suggests that this stadium endures for at least twelve months. If each instar were to be equally long-lived, the whole life cycle of *C. kochii* would extend over at least five years.

The scarcity of third and fourth instars in most population samples is difficult to explain. Only in the January and March–April 2004 samples were significant numbers of third instar nymphs present (Figure 28). If, as it seems, the life cycle occupies several years, then the absence or scarcity of a particular stage in the population could simply reflect a past year in which fewer eggs were laid or in which mortality of early stages was heavy. In order to gain a clearer and more reliable picture of population structure and change through the year, it will be necessary to gather larger samples. In this study, excavation by spade greatly restricted the area of soil that could be turned over, especially at greater depths. Additionally, it is possible that vibrations caused by digging might have caused some larger specimens to flee the excavation sites via existing galleries. Rearing specimens in captivity will also be necessary to determine longevity in the various instars and reliable data on longevity is necessary to interpret population structure.

Fecundity

Females have ten ovarioles per oviduct. Although a maximum of 14 eggs ready to lay were found in one individual (kept captive in a small container of soil for several weeks and therefore prevented from ovipositing) no more than seven were found in several other adult females. As each egg is laid singly in its own chamber, the rate of egg production must be comparatively low. What is not known is how long females go on ovipositing and how many eggs they would lay in their lifetime.

Mating

No observations of mating were made. Attempts to induce copulation by placing pairs of adults together in small containers proved unsuccessful. However, examination of the copulatory organs of freshly killed adults strongly suggests that mating individuals must come together 'tail' to 'tail' and venter to venter (somewhat as in Figure 20). The phallus cannot be exserted very far and has little flexibility. By making contact as in Figure 20, the hooks on the paraprocts of the male could engage the hind margin of sternite 8 of the female, pulling it down to open the vagina and the phallus would be orientated at just the right angle to permit intromission.

Copulation could hardly occur within the confines of normal galleries but it might occur in the widened sections of galleries noted under *Burrowing* above. Alternatively, copulation might occur on the surface of the ground. To check this possibility, nocturnal searches by torch-light were undertaken where sandgropers were known to be present in dense populations. Searches were made in both wet and dry weather conditions but no surface activity was encountered.

Predators, Parasites and Associated Organisms

According to several farmers, 'crows' (actually ravens) gather in flocks to predate on sandgropers turned out of the soil during ploughing of pastures. Johnstone and Storr (2004) recorded sandgropers from the guts of the Australian Raven. Farmers also report that foxes dig sandgropers from their surface trails and one observer noted the remains of sandgropers in fox scats.

This study found no evidence that sandgropers (either adults or immatures) are subject to attack by insect predators or parasitoids. If truly free of such attacks they would be a rarity among the insects. Evidently, their wholly subterranean existence, perhaps combined with their very hard integuments (anteriorly) and their chemical defences, serve to shield them from such enemies.

Gregarines

The mid guts of many specimens of *C. kochii* and *C. tindalei* were found to contain white bodies up to 2 mm long which superficially resembled insect ova or maggot-like larvae. These proved to be 'gamonts' of protistan parasites of the genus *Gregarina*, class Apicomplexa (formerly Sporozoa). They were present in varying numbers, rarely just one or two, frequently dozens and occasionally hundreds when they packed the lumen of the midgut. Another stage in the life cycle of these organisms, the spherical 'gamontocyst', was observed frequently in faecal pellets in the rectum. Gregarines were found in both adults and nymphs of various sizes from all study sites. Their incidence was comparatively low among dissected specimens collected from May to August, 16 of 50 *C. kochii*

and 3 of 18 *C. tindalei* being infested. Their incidence was very much higher in the early December sample of *C. kochii* from the Dandaragan site, 32 of 38 dissected specimens being infested. However, at the same site, only 3 of 30 dissected specimens from late January and none of 30 from late March/early April were infested. This dramatic reduction could be correlated perhaps with the apparent cessation or significant reduction of feeding observed in summer populations (see under *Food and Feeding*).

Amoebae

Specimens of *C. kochii* collected from the Dandaragan site in summer months exhibited another protistan occupant of the midgut: gold-coloured, single-celled organisms tentatively identified as amoebae. These occurred in varying numbers from just a few up to hundreds in the peritrophic membranes of the mid gut (made more visible by the absence of food material). It appeared that the amoebae did not survive their passage through the gut. Instead, they broke down in the posterior part of the mid gut or in the hind gut where they became concentrated in mucus-like material in narrow peritrophic membrane tubules. In the rectum, the tubules became convoluted and compacted into soft, translucent, honey-coloured pellets. Specimens whose rectal contents consisted only of convoluted tubules almost invariably had amoebae in the mid gut and their intestines were either devoid of food material or contained only minor quantities. Convoluted tubules were noted in 60% of summer-collected specimens (see Table 4 for details). These observations suggest that infestation of the gut by amoebae is associated with (perhaps even causes) a cessation of feeding. Given the absence of feeding, the amoebae are possibly ingested through the imbibition of ground-water (made possible by heavy summer rains). Because the amoebae appear not to survive their passage through the sandgropers, they cannot be considered to be parasites.

Nematodes

Nematodes identified as 'dauers' (non-feeding, resting or dispersal stage larvae) of the family Rhabditidae and possibly the genus *Rhabditis* (Dr Kerrie Davies, pers. comm.) proved to be common occupants of the genital chambers of *C. kochii* and *C. tindalei* in the northern parts of their ranges (north of the latitude of Geraldton). No such genital occupants were found in specimens south of Geraldton. In one specimen of *C. kochii*, dauers occurred also in a depression of the fore femur.

Only about 0.5 mm in length, dauers frequently formed tightly packed masses comprised of dozens or even hundreds of individuals beneath the phallus of male hosts. Dauers were also found in the vaginas of three adult females. When a freshly killed male sandgroper was dissected in saline solution, the nematodes were at first still but, on being disturbed with a needle, quickly became active, flexing their bodies strongly back and forth and dispersed in the saline. In some cases, however, a few to many of the nematodes were dead, brown and stiff.

Only occasional nematodes were encountered among gut contents and were possibly accidentally ingested with the food. None were encountered elsewhere among the internal organs of the insects. At the Dandaragan site, two egg chambers contained dead detached eggs with clusters of nematodes of various sizes on, in and around the latter. These nematodes were identified as bacterial-feeding cephalobids (common soil inhabitants) and an unidentified species, possibly *Mesorhabditis* (Dr Kerrie Davies, pers. comm.). Neither kind represented the same species as the dauers in the sandgropers' genital tracts.

As sandgropers carried dauers only in part of their range and no other part of this particular nematode's life cycle was found to be closely associated with the insects, the nematodes may simply be using them as dispersal agents. Questions remaining unanswered are – how do so many dauers find their way into the genital chambers, where do they come from and are the dauers transferred between the sexes during copulation? Sexual transmission of nematodes has been reported to occur in certain other orthopterans (e.g., Luong *et al.* 2000).

Mites

Phoretic deutonymphs (non-feeding, dispersal stage nymphs, also known as hypopi) of six species of mites were found externally on a number of individuals of *C. kochii* and *C. tindalei*. They occurred, sometimes singly, sometimes clustered, on various sheltered parts of the body: inner sides of fore legs, flanks of abdomen beneath mid and hind femora, and in folds of abdominal segments. These mites were identified by Dr Barry O'Connor (pers. comm.) and their names and host associations are listed in Table 6. Dr O'Connor noted that some members of unnamed genus 1 are associated with termites in the USA and central America while unnamed genus 2 is similar to taxa (e.g., *Forcellinia*) associated with ants and termites.

Fungi

Many dead eggs were found in chambers during excavation at the Dandaragan site in July and most of these were heavily coated with various kinds of fungi. Even seemingly fresh, suspended eggs often had fungal hyphae (bright yellow, black or colourless) growing over their surfaces and some were dotted with fungal sporangia.

Table 6 Mites recorded from the bodies of sandgropers in the present study.

Mite taxa	*C. kochii*	*C. tindalei*
Order Acariformes: Suborder Astigmata		
Acaridae – unnamed genus 1	+	
Acaridae – unnamed genus 2, species 1		+
Acaridae – unnamed genus 2, species 2	+	
Acaridae – *Sancassania* sp.	+	
Histiostomatidae, *Histiosoma* sp.		+
Order Parasitiformes: Suborder Mesostigmata		
Ascidae? (*Lasioseius*?)	+	

Defences

No biting or other defensive behaviours were observed while handling specimens except that, when restrained, the insects sought to 'burrow' their way to freedom with their powerful fore legs. When exposed during excavation, the insects always attempted to burrow back into the soil or withdrew into their galleries.

The characteristic odour produced by sandgropers (see above under *Odour glands*) probably serves a defensive function.

CONCLUSION

Many Tridactyloidea are heavily dependent on fresh-water bodies for their survival. Some 'pygmy mole crickets and mud crickets' (Tridactylidae and Ripipterygidae, resp.) inhabit the margins of lakes, streams and rivers, often in humid tropical environments, where they burrow and feed in the damp surface layers of mud or sand (Günther 1994). The Argentinian cylindrachetid, *Cylindroryctes spegazzinii* (Giglio-Tos), lives in the gritty shores of lakes and associated rivers (Günther 1992). *Cylindraustralia* species, however, live well away from free water and many inhabit semiarid to arid habitats. Nevertheless, the present study has indicated that they are still dependent on soil moisture and no specimens were ever found in truly dry soil.

Despite the gains from the present study, many basic questions concerning cylindrachetid biology remain to be answered, even for the principal subject *C. kochii*. For example, how long is the complete life cycle? How long do adults survive? Where, when and how do they mate? How many eggs does a female produce in her lifetime? Are there any insect predators or parasitoids not found in this study? At what rates do sandgropers burrow near the surface and at depth? Do they continually burrow into fresh soil or do they (at least at times) return to home burrows? Do they exhibit daily patterns of activity?

ACKNOWLEDGEMENTS

This study was made possible by the generous assistance of many individuals. While I cannot name all of those who provided me with specimens I am deeply grateful to the following for their interest, support, and hospitality during work on their properties: Paul Bloomer of Mullaloo (Perth); Ian and Denise Edgar of Annamullah farm, Dandaragan; Ross and Nola Johnson of Willi Gulli farm, Horrocks; Margaret, Bruce, and Keith Quicke of Eurardy Station; and Maurice and Dezi Webb, Chapman Valley east of Northampton. Voluntary assistance was generously provided by Otto Mueller (fieldwork) and Nihara Gunawardene (data entry and specimen mensuration). For the identification of organisms found in association with sandgropers and for information about them I am indebted to the following: Kerrie Davies, Waite Campus, University of Adelaide (nematodes); Barry O'Connor, University of Ann Arbor, Michigan, (mites); Neale Bougher, CSIRO Forestry, Perth, and Elaine Davison, Curtin University of Technology (both fungi). For encouragement, information and suggestions of useful references I wish to thank Kurt Günther, David Rentz, and Marlene Zuk. David Ragge provided guidance on numbering the nymphal stages. David Rentz and Winston Bailey kindly read an early draft of this paper and made useful suggestions for its improvement.

REFERENCES

Barrett, C. (1928). Notes on *Cylindracheta*. *Victorian Naturalist* **44**: 266–267.

Common, I.F.B. (1990). *Moths of Australia*, Melbourne University Press, Carlton, Victoria.

CSIRO (1991). *The Insects of Australia. A textbook for students and research workers* (Second edition), Melbourne University Press, Carlton, Victoria.

Flook, P.K., Klee, S. and Rowell, C.H.F. (1999). Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. *Systematic Biology* **48**: 233–53.

Gambardella, L.A. de (1971). Oviposicion y eclosion de *Rhipipteryx notata* Burm. 1838. *Revista Peruana de Entomologia* **14**: 282–285 (cited by Günther (1994); not seen).

Günther, K.K. (1992). Revision der Familie

Cylindrachetidae Giglio-Tos, 1914 (Orthoptera, Tridactyloidea). *Deutsche Entomologische Zeitschrift* **39** (4/5): 233–291.

Günther, K.K. (1994). Die Tridactyloidea-Fauna Kolumbiens (Orthoptera, Caelifera). *Deutsche Entomologische Zeitschrift* **41**(1): 45–56.

Johnstone, R.E. and Storr, G.M. (2004). *Handbook of Western Australian birds. Volume II. Passerines (blue-winged pitta to goldfinch).* Western Australian Museum, Perth.

Kevan, D.K.M. (1989). Grigs that dig and grasshoppers that grovel. *Revue d'Ecologie et de Biologie du Sol* **26**: 267–289.

Lawrence, J.F. and Britton, E.B. (1994). *Australian Beetles*, Melbourne University Press, Carlton, Victoria.

Luong, L.T., Platzer, E.G., Zuk, M. and Giblin-Davis, R.M. (2000). Venereal worms: sexually transmitted nematodes in the decorated cricket. *Journal of Parasitology* **86**: 471–477.

Rentz, D.C.F. (1996). *Grasshopper Country: the abundant orthopteroid insects of Australia.* University of New South Wales Press, Sydney.

Richards, K.T. (1980). The sandgroper – a sometimes not-so-friendly Western Australian. *Journal of Agriculture - Western Australia* **21**: 52–53.

Schremmer, F. (1972). Ein Massenvorkommen von bodenbewohnenden *Rhipipteryx forceps* (Tridactyloidea) in den kolumbianischen Anden. *Pedobiologia* **12**: 317–322 (cited by Günther (1994); not seen).

Tindale, N.B. (1928). Australian mole crickets of the family Gryllotalpidae (Orthoptera). *Records of the South Australian Museum* **4**: 1–42.

Urquhart, F.A. (1973). Some notes on the sand cricket (*Tridactylus apicalis* Say). *Canadian Field-Naturalist* **51**: 28–29 (cited by Günther (1994); not seen).

Uvarov, B. (1966). *Grasshoppers and Locusts, a Handbook of General Acridology*, vol. 1, Cambridge University Press, Cambridge

Wiley, T. (2000). Insect pests of the perennial fodder shrub tagasaste. Farmnote 48/2000, Western Australian Department of Agriculture, Perth.

Zuk, M. (1987). The effects of gregarine parasites on longevity, weight loss, fecundity and developmental time in the field crickets *Gryllus veletis* and *G. pennsylvanicus*. *Ecological Entomology* **12**: 349–354.

Manuscript received 7 December 2005; accepted 10 July 2006

Records of the Western Australian Museum **23**: 235–240 (2007).

Temporal variation in ground-dwelling invertebrate biomass in the Goldfields of Western Australia

Scott A. Thompson[1,2] and Graham G. Thompson[2,3]

[1,2] ATA Environmental, Dilhorn House, 2 Bulwer Street, Perth, Western Australia 6000, Australia (present address)

[2,3] Centre for Ecosystem Management, Edith Cowan University, Joondalup Drive, Joondalup, Western Australia 6027, Australia

[3] Corresponding author. Email: g.thompson@ecu.edu.au,

Abstract – We examined temporal variation in invertebrate biomass based on pit-trapping data from the semi-arid goldfields region of Western Australia (W.A.). Invertebrate dry biomass varied significantly among taxa, seasons and from year-to-year. There was a peak in dry biomass for all taxonomic groups from September to January that was followed by a significant decline for most families by April, and invertebrate biomass was lowest in mid-winter. For Araneae, Blattodea, Scorpionida and Chilopoda there was a significant rapid decline by April, whereas for Coleoptera, Orthoptera and Isopoda the rate of decline was slower. Other than during the winter survey, the dry biomass of Formicidae was unchanged. Chilopoda and Blattodea constituted the highest proportion of the biomass captured and the dry mass of individuals from these taxa was generally higher than that for the other invertebrate taxa. There was a positive correlation between invertebrate biomass and the number of reptiles caught but not with the number of mammals caught.

INTRODUCTION

Invertebrates are important in the functioning of nearly all natural environments and a change in their diversity and abundance can potentially affect the whole ecosystem. One potential impact that stems from their importance is as a prey source for reptiles, some small mammals (e.g., dasyurids) and many birds. Invertebrates are also increasingly being used as indicators of rehabilitation success in a variety of situations (Andersen 1994; Bisevac and Majer 1998, 1999a, 1999b; Lobry de Bruyn 1999; Madden and Fox 1997; Majer and Brown 1997; McGeoch 1998). All too often, one-off surveys are undertaken for terrestrial fauna at a particular site, and the data are used to characterise species richness and abundance or to provide benchmarks against which future impacts on the faunal assemblages are assessed. Such surveys pay little attention to temporal variation (Cowan and How 2004; Thompson and Thompson 2005a).

Our objective here was to: a) characterise seasonal patterns in invertebrate biomass; b) compare seasonal patterns in the Goldfields with those that have been described elsewhere in W.A.; and c) relate invertebrate biomass to the activity of insectivorous vertebrates.

METHODS AND SITES

We sampled the invertebrates on six occasions (Dec 2000, Jan 2001, April 2001, June 2001, Sept 2001 and Dec 2001) in nine undisturbed sites near Ora Banda (30°27'S, 121°4'E; approximately 50 km north of Kalgoorlie, W.A.) to establish the annual cycle of variation in biomass.

Ora Banda lies on Archaen granites that underlie lateritic gravel soils. The vegetation was heterogenous, ranging from Eucalypt-Casuarina-Mulga woodlands interspersed with *Acacia*, to sparsely distributed spinifex (*Triodia* spp.) and shrubs (*Acacia* spp.) to dense shrubs (*Acacia* spp., *Atriplex* spp., *Allocasuarina* spp.). The nine undisturbed areas were located in different habitats based on major vegetation types identified for the area by Mattiske Consulting (1995).

Other researchers sampling invertebrates have used small pit-traps filled with a preservative (Andersen *et al.* 2003; Bisevac and Majer 1999a, 1999b; Brennan *et al.* 1999). However, based on results of a pilot trial in September 2000, larger invertebrates (e.g., beetles, centipedes, spiders) were not easily caught in small diameter (~ 40mm) vials filled with a preservative. Therefore, 20 L pit-trap buckets without a preservative were

used for surveying the ground-dwelling invertebrates.

Eight pit-trapping lines, each containing three 20 L PVC buckets and three 150mm PVC pipes (600mm deep) that were used as pit-traps, were alternated and evenly spaced along 30m long fly-wire drift fences (250mm high) at each of the nine study sites. Each trapping line was approximately 20m apart. Invertebrates were collected daily using forceps from each of the 20 L pit-trap buckets, for six days for each of the six survey periods. Invertebrates were not collected from the PVC pipe pit-traps. These same pit-traps were used for surveying reptiles and small mammals (see Thompson *et al.* 2003; Thompson and Thompson 2005b). We appreciate that captured vertebrates or other invertebrates may have eaten some of the invertebrates caught in these pit-traps, but we believe that the number destroyed would be low compared to the total abundance, as pit-traps were cleared each morning. Small invertebrates, and in particular ants that died and dehydrated in the pit-traps, were very difficult to collect at the bottom of the buckets. As a consequence, we would have under-sampled the very small invertebrates; however, this will have had little consequence on our estimate of temporal variation in terrestrial invertebrate biomass given the magnitude of these variations.

All invertebrates collected were initially preserved in 70% ethanol. The preserved invertebrates were later sorted into the following groups: Formicidae (ants); Coleoptera (beetles); Chilopoda (centipedes); Blattodea (cockroaches); Orthoptera (grasshopper and crickets); Isopoda (slaters); Scorpionida (scorpions); Araneae (spiders) and others. These particular invertebrate groups were chosen because they are easily identified in reptile and mammal stomach contents and were consistent with how other authors report reptile stomach content data (e.g., Pianka 1986).

The invertebrate catch from all 24 PVC buckets at each site on each day were grouped. All invertebrates were removed from alcohol, placed into vials and dried for four days at 35°C in a controlled temperature room under fan-forced airflow. Four days was sufficient to remove the moisture and reach a constant mass. The time taken to dry invertebrates was tested after the first survey period in December 2000. There was no change in invertebrate mass between the third and fourth days of drying. The number of individual invertebrates in each group was counted and all samples were weighed to four decimal places using electronic scales.

Data analysis

The dry biomass of invertebrates was used for all calculations. Variation in invertebrate biomass among the six survey periods was examined using a full factorial ANOVA [Biomass (g/24 pit-trap nights) = site + taxonomic group + survey period + site*group + site*survey period + taxonomic group*survey period + site*taxonomic group*survey period] using statistiXL (http://www.statistiXL.com/; V.1.5). Variance in the ANOVA model came from differences among the six days of data for each site for each survey period.

Correlation coefficients were calculated to demonstrate relationships between the total invertebrate dry biomass for invertebrate group and the number of reptiles and mammals caught during each survey period. In addition, the number of small dasyurids caught was correlated with invertebrate dry biomass, as they are almost exclusively insectivorous. Significance level at $\alpha = 0.05$ was used for all analyses.

RESULTS

During six surveys (7776 pit-trap nights) from December 2000 to December 2001, 15069 individual invertebrates were captured with a total dry body mass of 1402.4 g. Chilopoda, Blattodea and Araneae constituted more than two thirds of the invertebrate biomass captured (Table 1). The 'other' group, which accounted for 9.8% of the total biomass, included gastropods, mantids, earwigs, stick-insects, moths and larvae. Coleoptera had a higher dry mass than Orthoptera, Isopoda and Scorpionida. The average dry mass for individuals was highest for Chilopoda and Blattodea (Table 1). Counting many of the small dehydrated ants proved to be an impossible task and their individual body mass was not able to be accurately assessed, but it was probably the lowest of the groups assessed.

Among seasons variation in invertebrate biomass

There was a significant difference among factors (e.g., seasons, taxonomic groups and sites), and a

Table 1 Average mass of individuals and proportion of the biomass represented by each group of invertebrates

Group	Mean individual dry mass (g)	Percentage of biomass
Formicidae		3.27
Coleoptera	0.121	11.87
Chilopoda	0.392	25.67
Blattodea	0.323	21.42
Orthoptera	0.076	4.42
Isopoda	0.020	1.78
Scorpionida	0.093	2.50
Araneae	0.090	19.30
Other		9.77

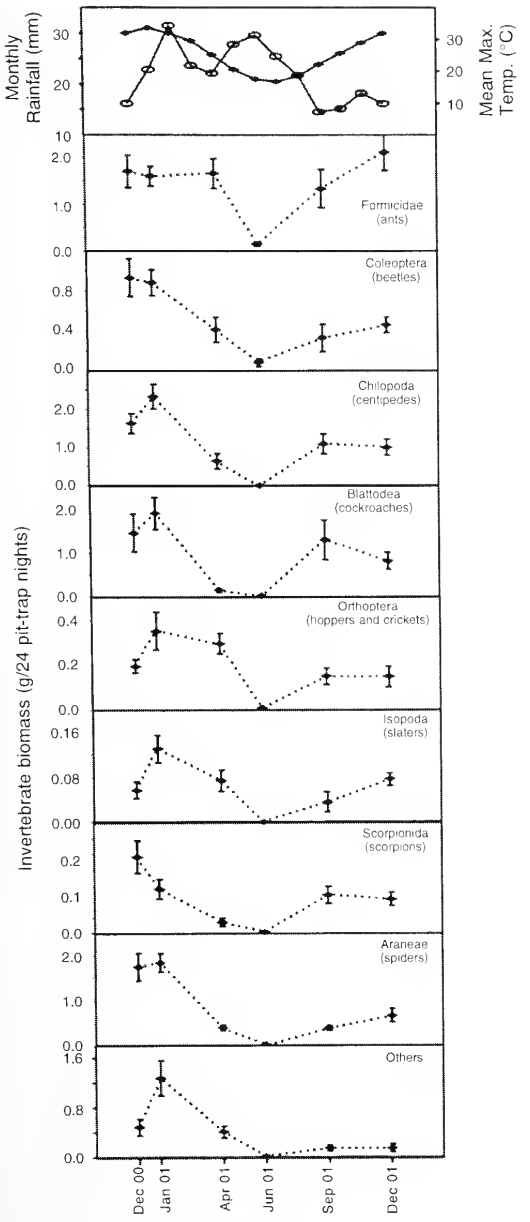


Figure 1 Mean dry biomass for each invertebrate group for each of the six survey periods showing means ± 1 se.

significant interaction among factors for invertebrate biomass (Table 2; Figure 1).

A post-hoc Tukey test after the full factorial ANOVA on all survey periods showed that December 2000 and January 2001 had a higher invertebrate biomass than all other survey periods, including December 2001 (Table 3). June 2001 had the lowest invertebrate biomass. December 2001 biomass was significantly less than December 2000 but the same as for April 2001 and September 2001 (Table 3). A post-hoc Tukey test indicated that Coleoptera and Araneae were the only two families that were significantly different between the two December surveys.

There was no significant difference between the biomass for any taxonomic group for the December 2000 and January 2001 survey periods. With the June catch removed from the dataset, the biomass of Formicidae was not significantly different among the seasons ($F_{3, 225} = 0.80$, $P = 0.53$), whereas for all other taxonomic groups there were significant differences in the dry biomass among seasons (Figure 1). Chilopoda, Blattodea, Scorpionida and Araneae all showed a significant reduction in dry biomass from the January to the April survey period. The decline from January to April was not significant for the other invertebrate groups, but it was significant from January to June. The variation in biomass for Orthoptera and Isopoda, and Chilopoda and Blattodea across the six survey periods were similar (Figure 1). Araneae dry biomass was high for the December 2000 and January 2001 survey periods, then remained low for the subsequent periods.

Abundance of reptiles and mammals relative to invertebrate biomass

There was a positive correlation between the biomass of Coleoptera, Chilopoda, Blattodea, Scorpionida and Araneae and the number of reptiles caught during each survey period, but the total number of mammals and the number of dasyurids caught were not significantly correlated to the dry invertebrate biomass for any of the families (Table 4).

Table 2 ANOVA results for comparison of variation in invertebrate biomass among sites, seasons and taxonomic groups.

Source	SS	Df	MSq	*F*-value	*P* value
Site	41.235	8	5.154	4.403	< 0.0001
Season	258.906	5	51.781	44.234	< 0.0001
Group	400.062	7	57.152	48.821	< 0.0001
Site*Season	90.821	40	2.271	1.940	< 0.0001
Site* Group	258.412	56	4.614	3.942	< 0.0001
Season* Group	257.958	35	7.370	6.296	< 0.0001
Site*Season*Group	399.909	280	1.428	1.220	0.011

Table 3 Variation in invertebrate mass (g/24 pit-trap nights) among survey periods. *P* values are from a post-hoc Tukey test after an ANOVA. Bold *P* values represent a significant difference.

Survey period	Mean ± se	December 2000	January 2001	April 2001	June 2001	September 2001
December 2000	0.803 ± 0.129					
January 2001	0.968 ± 0.139	0.22				
April 2001	0.273 ± 0.040	**< 0.01**	**<0.01**			
June 2001	0.020 ± 0.006	**<0.01**	**<0.01**	**<0.01**		
September 2001	0.443 ± 0.080	**<0.01**	**<0.01**	0.19	**<0.01**	
December 2001	0.436 ± 0.059	**<0.01**	**<0.01**	0.23	**<0.01**	~1.0

Table 4 Correlation between invertebrate family biomass and the number of reptiles and mammals caught during the six survey periods. Bold *P* values represent a significant correlation.

	Formicidae	Coleoptera	Chilopoda	Blattodea	Orthoptera	Isopoda	Scorpionida	Araneae
Reptiles	0.558	0.963	0.984	0.913	0.703	0.739	0.873	0.975
Mammals	0.414	0.510	0.203	0.214	0.041	-0.006	0.663	0.414
Small dasyurids	0.474	-0.152	-0.274	-0.188	-0.305	-0.165	0.111	-0.275
P values								
Reptiles	0.250	**0.002**	**<0.001**	**0.011**	0.119	0.093	**0.023**	**0.001**
Mammals	0.415	0.301	0.699	0.684	0.939	0.992	0.152	0.415
Small dasyurids	0.342	0.774	0.599	0.721	0.557	0.755	0.834	0.599

DISCUSSION

In the south-west of W.A. there have been a few phenological investigations of invertebrate activity. Majer and Nichols (1998) reported that the number of ants showed appreciable intra- and inter-specific variation over a 14 year period in the forested areas of south-western Australia, with detectable patterns not clearly evident. Postle (1985) reported soil and litter invertebrate numbers around Dwellingup in the south-west of Australia being highest in autumn and progressively declining to a low in December before beginning to increase in February. In contrast, Majer (1985b) and Majer and Koch (1982) reported herbivorous invertebrate numbers were negatively correlated with rainfall at sites at Perth, Dwellingup and Manjimup in the south-west of Australia with lowest numbers in winter, and higher levels of activity in spring, summer and early autumn. Predator insects at the Perth site were most active from late autumn to early spring (Majer and Koch 1982) and low in summer, whereas invertebrate numbers were lowest at Dwellingup in May and June, and at Manjimup in June and July (Koch and Majer 1980). The invertebrate decomposers were most active in winter and spring at the two most northerly sites (Perth and Dwellingup), but at Manjimup, they were most active during summer (Koch and Majer 1980). At Katanning in the wheatbelt to the east of these three sites (e.g., Perth, Dwellingup and Manjimup), ants were most active during the December to March period (Majer 1985a). In the arid Tanami desert, Paltridge and Southgate (2001) reported significant fluctuation in invertebrate biomass between survey periods, with the lowest catch rates being recorded in winter.

Ora Banda is in the semi-arid Goldfields region of W.A. and receives regular winter rain (May to July), and thunderstorms and irregular heavy rain resulting from decaying cyclones and low pressure systems that cross the W.A. coast in the Pilbara during late summer (Figure 1). Summer rain can cause local flooding and leave ephemeral ponds for weeks. Mean monthly maximum summer temperatures are in the low 30s and drop to the low 20s in winter (Figure 1).

The most obvious general feature of invertebrate biomass around Ora Banda was the higher biomass for all families during the summer of 2000/01 and the steady decline into winter and an increase in the following spring. There was no difference in the dry biomass for any taxonomic groups between December 2000 and January 2001. For Coleoptera, Chilopoda, Blattodea, Scorpionida and Araneae, the very obvious peak (Figure 1) in dry biomass during December-January was followed by a significant decline by April and a further drop to June. For Orthoptera and Isopoda, the rate of decline was slower, but the dry biomass for these species was very low in June. For Formicidae, there was no difference among the five survey periods when the June data were excluded. There was no difference in dry biomass for any taxonomic group between September and December 2001, but the overall biomass was higher in December 2000 than in December 2001. These data suggest that the biomass of invertebrates increases rapidly at the end of winter. It then remains the same from September to

January, and then declines to a low value in mid winter. This is similar to that reported by Majer (1985a) for the semi-arid wheatbelt and Paltridge and Southgate (2001) for the arid Tanami Desert. At other sites in the more mesic south-west of W.A. the pattern seems more variable and perhaps linked to foraging strategy and diet.

Reptiles were most active when the invertebrate biomass was high. This might be expected as a majority of the reptiles around Ora Banda eat invertebrates and, for many, invertebrates are their primary prey. However, many of the small mammals caught (e.g., *Cercartetus concinnus, Mus musculus, Pseudomys bolami, P. hermannsburgensis*) either do not eat invertebrates or they constitute only a small proportion of their diet, and the activity patterns for these species is probably not linked to invertebrate abundance. In contrast, most of the small dasyurids are almost exclusively insectivorous, and it might be expected that their behaviour and activity patterns are linked to invertebrate abundance. However, there was no correlation between the number of small dasyurids caught during each survey period and dry invertebrate biomass. It would therefore be expected that body condition of dasyurids around Ora Banda would be lower in winter when invertebrates were scarce, and they would put on weight in summer because of the increased food supply, and this would be when they are likely to be reproductively active.

Chilopoda and Blattodea constitute the highest proportion of the biomass captured, and the dry mass of individuals was higher than for other invertebrate taxa. Centipedes and cockroaches are generally nocturnal and are therefore probably an important prey source for many of the small mammals in the area. Spiders are also relatively plentiful and vary in dry body mass, providing a range of prey sizes for reptiles, amphibians and small mammals that prey upon them.

Given varying seasonal and year-to-year fluctuations for different invertebrate taxa, the use of the abundance of invertebrates as a bio-indicator of ecosystem restoration should be undertaken with considerable caution. In most circumstances where a faunal assemblage is used as a bio-indicator, there is a presumption that most of the variance in abundance and species richness is directly related to ecosystem development and not environmental or variables unrelated to the restoration success (Thompson and Thompson 2005b). A single terrestrial survey of invertebrates is only able to describe the assemblage for a particular period in time, as relative abundance varies both seasonally and from year-to-year. Therefore, in circumstances where invertebrate monitoring data are used to measure the success of a restoration area compared with an adjacent undisturbed area, the two areas must also be surveyed simultaneously. In most circumstances, our current level of knowledge is such that we cannot separate natural year-to-year variation in invertebrate assemblages or biomass from variations attributable to stochastic events such as fire, grazing, drought or unseasonally heavy or no rainfall.

ACKNOWLEDGEMENTS

This research was undertaken with ethics approval granted by Edith Cowan University and licences issued by the Department of Conservation and Land Management. This research was financially supported by OMG Cawse Nickel and Barrick Kanowna, for which we are very appreciative.

REFERENCES

Andersen, A. N. (1994). Ants as Indicators of Restoration Success Following Mining in Northern Australia. *In 1994 AusIMM Annual Conference. Australian Mining Looks North – The Challenges and Choices. 5–9 August 1994*. Australian Institute of Mining and Metallurgy, Darwin.

Andersen, A. N., Hoffmann, B. D. and Somes, J. (2003). Ants as indicators of minesite restoration: community recovery at one of eight rehabilitation sites in central Queensland. *Ecological Management and Restoration* **4 Sup**: S12–S19.

Bisevac, L. and Majer, J. D. (1998). Invertebrates as success indicators for mine site rehabilitation. *In* C. J. Asher and L. C. Bell (eds), *Proceedings of the Workshop on Indicators of Ecosystem Rehabilitation Success 23–24 October*. Australian Centre for Mining Environmental Research, Melbourne.

Bisevac, L. and Majer, J. D. (1999a). Comparative study of ant communities of rehabilitated mineral sand mines and heathland, Western Australia. *Restoration Ecology* **7**: 117–126.

Bisevac, L. and Majer, J. D. (1999b). An evaluation of invertebrates for use as success indicators for minesite rehabilitation. *In* W. F. Ponder and D. Lunney (eds), *The other 99%: The conservation and biodiversity of invertebrates*: 46–49. Transactions of the Royal Zoological Society of New South Wales: Sydney.

Brennan, K. E. C., Majer, J. D. and Reygaert, N. (1999). Determination of an optimal pitfall trap size for sampling spiders in a Western Australian Jarrah forest. *Journal of Insect Conservation* **3**: 297–307.

Cowan, M. A. and How, R. A. (2004). Comparisons of ground vertebrate assemblages in arid Western Australia in different seasons and decades. *Records of the Western Australian Museum* **22**: 91–100.

Koch, L. E. and Majer, J. D. (1980). A phenological investigation of various invertebrates in forest and woodland areas in south-west of Western Australia. *Journal of the Royal Society of Western Australia* **63**: 21–28.

Lobry de Bruyn, L. A. (1999). Ants as bioindicators of soil

function in rural environments. *Agriculture, Ecosystems and Environment* **74**: 425–441.

Madden, K. E. and Fox, B. J. (1997). Arthropods as indicators of the effects of fluoride pollution on the succession following sand mining. *Journal of Applied Ecology* **34**: 1239–1256.

Majer, J. D. (1985a). Seasonality of ants (Formicidae) in south-western Australia. *In* P. Greenslade and J. D. Majer (eds), *Soil and litter invertebrates of some Australian Mediterranean-type ecosystems*, School of Biology, Bulletin number 12, Western Australian Institute of Technology, Perth.

Majer, J. D. (1985b). Seasonality of epigaeic invertebrates at Perth, Dwellingup and Manjimup. *In* P. Greenslade and J. D. Majer (eds), *Soil and litter invertebrates of some Australian Mediterranean-type ecosystems*, School of Biology, Bulletin Number 12, Western Australian Institute of Technology, Perth.

Majer, J. D. and Brown, E. (1997). The role of invertebrates in ecological functioning. *In* C. J. Asher and L. C. Bell (eds), *Fauna habitat reconstruction after mining, 10–11 October 1997*, Australian Centre for Mining Environmental Research, Adelaide.

Majer, J. D. and Koch, L. E. (1982). Seasonal activity of hexapods in woodlands and forest leaf litter in the south-west of Western Australia. *Journal of the Royal Society of Western Australia* **65**: 37–45.

Majer, J. D. and Nichols, O. G. (1998). Long-term recolonisation patterns of ants in Western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success. *Journal of Applied Ecology* **35**: 161–182.

Mattiske Consulting Pty Ltd (1995). *Flora and vegetation of the Cawse find area*, Woodward-Clyde, Perth.

McGeoch, M. A. (1998). The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews of the Cambridge Philosophical Society* **73**: 183–201.

Paltridge, R. and Southgate, R. (2001). The effect of habitat type and seasonal conditions on fauna in two areas of the Tanami Desert. *Wildlife Research* **28**: 247–260.

Pianka, E. R. (1986). *Ecology and natural history of desert lizards: Analyses of the ecological niche and community structure*, Princeton University Press, Princeton.

Postle, A. C. (1985). Density and seasonality of soil and litter invertebrates at Dwellingup. *In* P. Greenslade and J. D. Majer (eds), *Soil and litter invertebrates of some Australian Mediterranean-type ecosystems*, School of Biology, Bulletin Number 12, Western Australian Institute of Technology, Perth.

Thompson, G. G., Thompson, S. A., Withers, P. C. and Pianka, E. R. (2003). Diversity and abundance of pit-trapped reptiles of arid and mesic habitats in Australia: Biodiversity for environmental impact assessments. *Pacific Conservation Biology* **9**: 120–35.

Thompson, S. A. and Thompson, G. G. (2005a). Temporal variation in reptile assemblages in the Goldfields of Western Australia. *Journal of the Royal Society of Western Australia* **88**: 25–36.

Thompson, G. G. and Thompson, S. A. (2005b). Mammals or reptiles, as surveyed by pit-traps, as bio-indicators or rehabilitation success for mine sites in the goldfields region of Western Australia? *Pacific Conservation Biology* **11**: 268–286.

Manuscript received 17 August 2005; accepted 24 August 2006

Records of the Western Australian Museum **23**: 241–257 (2007).

A new species of rock-dwelling hylid frog (Anura:Hylidae) from the eastern Kimberley region of Western Australia

Paul Doughty[1*] **and Marion Anstis**[2]

[1]Department of Terrestrial Vertebrates, Western Australian Museum, 49 Kew Street, Welshpool WA 6106, Australia
*corresponding author – e-mail: Paul.Doughty@museum.wa.gov.au

[2]26 Wideview Road, Berowra Heights NSW 2082, Australia

Abstract – Australia's documented frog diversity slowly continues to grow owing to genetic tests for cryptic species and ongoing exploration of remote regions. Recent collecting trips in Western Australia's east Kimberley region resulted in the discovery of a new rock-dwelling hylid frog, *Litoria staccato* sp. nov. The new species is closely related to the much more widely distributed *L. coplandi*, which also breeds in the same rocky creeks. *Litoria staccato* sp. nov. is a small to moderate-sized frog characterised from co-occuring species by a combination of a moderately pointed snout, expanded terminal discs, half-webbed toes and a mottled appearance with variable colouration (reddish brown, grey or beige). The advertisement call consists of a rapid burst of irregularly-spaced notes, followed by groups of softer calls comprised of single or complex notes. Compared to *L. coplandi*, *L. staccato* sp. nov. is slightly smaller, has reduced webbing between the toes, different colouration and pattern (including diffuse vertebral and dorsolateral stripes), reduced glandular tissue at the angle of the jaw and a highly divergent call. Tadpoles show some adaptations to stream-living but also have body shape affinities associated with ground hylid pond-dwelling types such as *L. inermis*. The new species has only been found near Wyndham in the far north of Western Australia, and no specimens have been detected in existing museum collections indicating a restricted distribution. Owing to its remoteness and complex geology, the Kimberley region may hold other undiscovered rock-dwelling species with small natural ranges.

Key words: frog, Kimberley, *Litoria*, rock-dwelling, tadpole

INTRODUCTION

Frogs of the genus *Litoria* are prominent among northern Australian vertebrate fauna. Here they have radiated into a diversity of forms specialized for different lifestyles, including species that are strongly associated with rocky streams and pools along escarpments. There are currently three small rock-dwelling hylids from the humid Kimberley to Arnhem Land region of northern Australia: *L. coplandi*, *L. personata* and *L. meiriana*. All three species have expanded terminal discs on their fingers and toes and are encountered along rocky creeks, water holes and escarpments. Tyler and Davies (1978) initially placed *L. coplandi* in its own monotypic species group. Barker *et al.* (1995) placed the rock-dwelling forms either directly in a *"L. latopalmata"* group (*L. personata*) or in "other *Litoria*" (*L. coplandi* and *L. meiriana*). Before being formally described, specimens of *L. coplandi* were placed in *"L. latopalmata watjulumensis"* but later described as a separate taxon by Tyler (1968a). Tyler *et al.* (1978) compared the new taxon *L. personata* to various *L. latopalmata* group members, but not to *L. coplandi*. Recent molecular work indicates that all three rock-adapted hylids may be only distantly related (S. Donnellan *personal communication*), suggesting that they evolved an association with flowing water and pools on rocks independently. *Litoria meiriana* is likely to be only distantly related to the other two species based on morphological (adults and tadpoles), behavioural and genetic differences (Tyler and Davies 1978; Tyler *et al.* 1983; S. Donnellan *personal communication*).

Potential threats to the native frogs of the tropical Kimberley region in Western Australia from introduced species such as the cane toad (*Bufo marinus*: Bufonidae) and chytrid fungus have generated concern about the future status of frogs there. As a result, new surveys are being conducted to estimate the true diversity of the region. Initial surveys conducted in the wet season of 2005–2006 in the east Kimberley have revealed a previously unknown taxon closely allied to, and syntopic with, the rock frog, *L. coplandi*. Here we describe this

taxon as a new species and present information on the male advertisement call, embryonic and tadpole development and the breeding habitat.

MATERIALS AND METHODS

We examined 12 adult specimens of the new taxon and compared them with its suspected close allies *L. coplandi* and *L. personata*. Morphological measurements generally follow Tyler (1968b) with some modifications (see Table 1). Measurements that could be made on either side of the body (e.g., tarsus length) were measured on the right side of the animal, unless this was damaged or misshapen. Measurements were made under a Leica MZ6 dissecting scope with digital vernier callipers to the nearest 0.01 mm. We also calculated the following ratios (see Table 1A for abbreviations): HL/HW, IN/IO, EN/IN, TL/SVL, TarL/SVL and TarL/TL.

We compared the calls of two males of the new species with the call of one *L. coplandi* and one *L. meiriana*. Calls were recorded on a Marantz PMD670 digital recorder with a BeyerDynamic M88N microphone. Sound analysis was carried out on Cool Edit Pro and Raven 1.3b (Charif *et al.* 2004).

We collected a sample of embryos just prior to hatching close to where calling males and a gravid female had been collected the previous night. Six hatchlings and a small sample of capsules from the same clutch were also preserved. A sample of live hatchlings was collected and reared to metamorphosis to confirm identity. In addition, another sample of small tadpoles at stages 26–27 (Gosner 1960) found in the same pool and

Table 1 Characters measured with abbreviations and explanations.

Character	Abbrev.	Explanation of Measurement
A. Adults		
Snout-vent length	SVL	From tip of snout to posterior tip of urostyle
Inter-limb length	ILL	From axilla to groin
Head length	HL	From tip of snout to posterior edge of tympanum
Head width	HW	Width of head at centre of tympani
Eye-naris distance	EN	From anterior corner of eye to posterior edge of naris
Interorbital span	IO	Distance between anterior corners of eyes
Internarial span	IN	Distance between inner edges of nares
Naris-mouth distance	NM	Posterior edge of naris to upper edge of jaw
Eye diameter	EL	Anterior to posterior corners
Tympanum length	TymL	Anterior to posterior edges
Forearm length	FL	Elbow to proximal edge of palmar tubercle
Hand length	HandL	Tip of 3rd finger to proximal edge of palmar tubercle
Third finger disc width	3rdFDW	Maximum transverse width of 3rd finger disc
Tibia length	TL	Measured with leg in natural resting position, from knee to tarsus
Tarsus length	TarL	Measured with leg in natural resting position, from proximal end of tarsus to proximal edge of inner metatarsal tubercle
Foot length	FootL	From tip of 4th toe to proximal end of inner metatarsal tubercle
Fourth toe disc width	4thTDW	Maximum transverse width of 4th finger disc
B. Tadpoles		
Total length	TL	From tip of snout to tail tip
Body length	BL	From tip of snout to end of body
Body depth	BD	Maximum height of body
Body width	BW	Widest point of body in dorsal view
Body width at eyes	EBW	Body width at level of eyes in dorsal view
Tail muscle depth	BTM	Depth of tail muscle at base
Tail muscle width	BTMW	Width across tail muscle at base in dorsal view
Tail depth	TD	Measured at midpoint of tail
Dorsal fin depth	DF	Measured at tail depth
Tail muscle depth	TM	Measured at tail depth
Ventral fin depth	VF	Measured at tail depth
Inter-orbital span	IO	Measured in dorsal view
Inter-narial span	IN	Measured in dorsal view
Eye to naris	EN	Measured in dorsal view
Narial diameter	N	Measured in dorsal view
Snout to spiracle	SS	
Snout to naris	SN	
Snout to eye	SE	
Eye diameter	ED	
Oral disc width	ODW	Measured at maximum in ventral view

considered likely to be this species, was collected and reared to metamorphosis. Tadpoles were reared in 50 cm diameter containers of stream water to a depth of 14 cm, rocks and leaf litter from the stream where they were collected. Water was aerated and temperatures ranged from about 16–36°C during development.

Tadpole descriptions follow Anstis (2002). Abbreviations for tadpole morphometric characters follow Anstis and Tyler (2005) and are given in Table 1B. Measurements were made with an ocular micrometer attached to a microscope and vernier callipers. Embryos and tadpoles were drawn with the aid of a camera lucida, and photographs of live tadpoles taken using a Nikon D70 and 60 mm macro lens.

SYSTEMATICS

Family HYLIDAE Rafinesque 1815

Genus *Litoria* Tschudi 1838

Litoria staccato sp. nov.

Chattering Rock Frog
Figures 1–5

Holotype

WAM R162611. Adult male collected near "The Grotto", 30 km south of Wyndham, Western Australia (15.72540°S, 128.27953°E), by P. Doughty and C. Mills on 30 January 2006. Liver sample stored at -75°C at the Western Australian Museum, Welshpool.

Paratypes

WAM R162512, R162514 (males) and WAM R162513 (female) collected 8 January 2006 by P. Doughty, J. Francis and M. Anstis (15.71466°S, 128.27288°E); WAM R162537-8 (males) collected on 15 January 2006 by P. Doughty, J. Francis and C. Mills (15.72506°S, 128.27951°E); WAM R162612-6 (males) and WAM R162620 (female) collected on 30 January 2006 by P. Doughty and C. Mills (15.72540°S, 128.27953°E). Liver samples stored at –75°C at the Western Australian Museum, Welshpool.

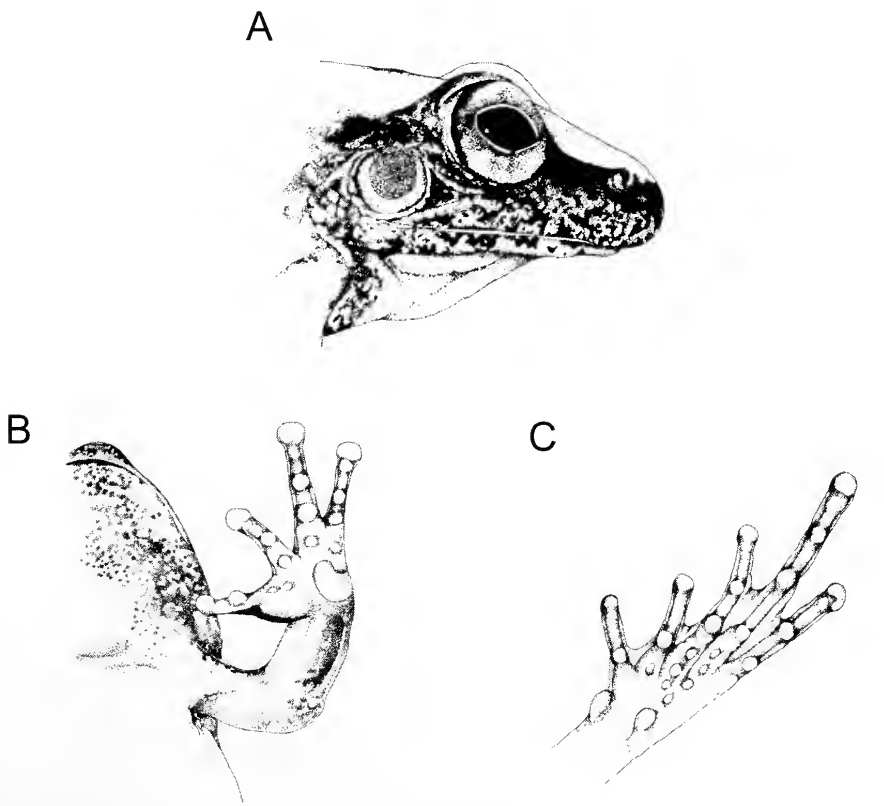


Figure 1 Head (A), chin and hand (B) and foot (C) of the male holotype of *Litoria staccato* (WAM R162611).

Embryos and Tadpoles

WAM R162946-7 (embryos), WAM R162948-57 (tadpoles) collected 9 January 2006 by M. Anstis and P. Doughty (15.71466°S, 128.27288°E).

Diagnosis

A small to moderate-sized rock-dwelling hylid with moderately pointed snout, medium build and slender limbs. Tips of fingers widely expanded and toes half-webbed. Dark lateral head stripe present but not clearly defined; pale triangular patch usually discernible on snout. Lateral head stripe continues beyond tympanum and fades posteriorly into broader mottled lateral stripe that demarcates lateral and ventral zones. Dorsal colour of males variable, ranges from reddish brown to slate grey to beige; females reddish brown. There are variably expressed diffuse darker vertebral, dorsolateral and lateral stripes.

Distinguishable from similar-sized ground hylid frogs of the Kimberley-Arnhem Land region by possession of broadly expanded discs on tips of fingers and toes (not *L. inermis*, *L. latopalmata*, *L. nasuta* or *L. pallida* which lack expanded terminal discs), toes half-webbed (not *L. coplandi*, *L. meiriana* or *L. wotjulumensis* which have fully webbed toes) and mottled dorsal colouration with diffuse lateral head stripe, vertebral and dorsolateral stripes (not *L. personata* which has strong lateral head stripe and uniform-coloured dorsum) (see also *Comparison with other species*, below). The male call consists of a series of rapid, high-pitched irregularly spaced notes, interspersed with short and complex softer calls (Figure 3C).

Description of holotype

Head narrow and triangular with moderately pointed snout and prominent eyes (Figure 1A). In profile, snout gradually narrows to oblique tip. Nares positioned on tip of snout under canthus rostralis, slightly oval, opening dorsolaterally and slightly forwards. Canthus rostralis straight with moderately sharp edge; loreal region steep-sided and concave. Tympanum prominent and circular, distinct annulus present except for dorsal edge. Small cluster of 5–6 glandular nodules between lower posterior edge of tympanum and insertion of forearm. Vomerine teeth a pair of smooth ridges anterior to medium-large oblique choanae. Tongue oval, tapers posteriorly, free edge blunt and unnotched.

Arms short and slender. Fingers long, slender and unwebbed but with weak lateral fringes (Figure 1B). Palmar tubercles at base of outer portion of wrist prominent and paisley-shaped (narrow end pointing towards fingers). Large tubercles present on finger joints with smaller tubercles on palm. Nuptial pad comprised of fine layer of small dark rugose tubercles on inner margin of 1st finger. Fingers in order of length: 3>4>1>2. Tips of fingers with broad discs: 1st and 2nd fingers approximately 2x wider, and 3rd and 4th fingers approximately 1.5x wider than distal phalanx in life (in preservative, discs 1.5x and 1x wider, respectively).

Legs long and slender. Distinct fold of skin above knee. A fringe runs along inner tarsus and connects to inner metatarsal tubercle. Moderate sized inner metatarsal tubercle narrow, projects distally (Figure 1C). Outer metatarsal tubercle small and oval, projects towards toes. Feet narrow. Toes in order of length: 4>5>3>2>1. Webbing between 1st and 2nd and between 2nd and 3rd toes to proximal end of distal phalanges on each toe. Webbing between 3rd and 4th toes to just beyond proximal joint of distal phalange on 3rd toe, and to base of proximal end of penultimate phalanx on 4th toe. Webbing between 4th and 5th toes to base of proximal end of penultimate phalanx on 4th toe and to just above proximal end of distal phalanx on 5th toe. Lateral fringes on all toes beyond webbing. Toe discs only slightly wider than penultimate phalanx in life (in preservative, approximately the same width). Medium conical subarticular tubercles on joints of toes with minute tubercles on plantar surface.

Skin on dorsum and limbs smooth. Belly granular with slight transverse crease between arms, towards anterior edge of arm insertion. Underside of posterior edge of thighs with larger flattened granulation. Coccyx forms prominent ridge that protrudes slightly beyond end of body. Cloaca positioned just below coccyx, projects dorso-posteriorly.

Dimensions of holotype (mm)

SVL 30.5; ILL 13.15; HL 11.66; HW 10.83; EN 2.76; IO 5.3; IN 3.21; NM 1.64; EL 3.21; TymL 2.30; FL 6.15; HandL 7.60; 3rdFDW 0.72; TL 15.72; TarL 8.40; FootL 11.69; 4thTDW 0.56; HL/SVL 0.38; HL/HW 1.08; EN/IN 0.86; EN/IE 0.52; TL/SVL 0.52; TarL/SVL 0.28; TarL/TL 0.53.

Colour in life

Dorsum light reddish brown (Figure 2A). Faint, darker, narrow vertebral and wider dorsolateral stripes present, the latter forming a diffuse border between dorsal and lateral zones. Lateral head stripes dark grey, not sharply defined along snout, with diffuse dorsal and ventral edges. Lateral head stripe begins narrowly at rostrum passing through nostril and lower half of eye; continues posteriorly from eye through tympanum, extending just above dorsal edge of tympanum; angles downwards towards ventral surface, fading diffusely just over half-way between insertion of arms and legs; continues as diffuse mottled border between lateral and ventral zones. A subtle, yet distinct, paler triangular patch on snout is defined dorsally by border of lateral head stripes and posteriorly by

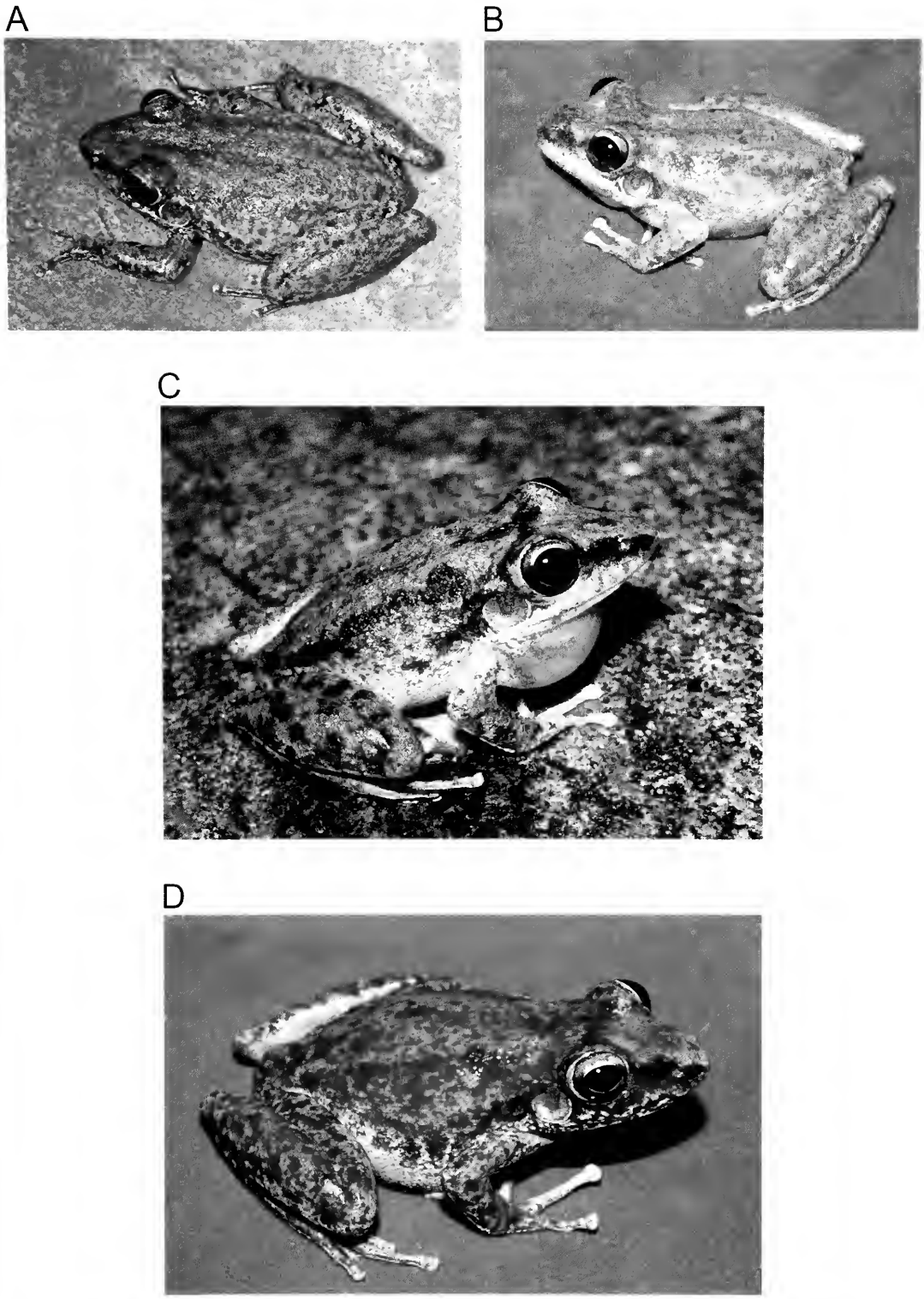


Figure 2 Adult frogs in life of *Litoria staccato* showing colour variation. A) holotype male (WAM R162611) with reddish brown colour, B) beige male (WAM R162514); C) calling slate grey male (uncollected), D) reddish brown female (WAM R162513).

diffuse darker bar between eyes. As triangular patch narrows towards tip of snout, it broadens slightly and contacts nares before terminating just anterior to nares. Lateral head stripes continue forward to join at rostrum tip. Upper lip mottled with diffuse black. Lower lip pale with dark mottling not extending to chin. Chin darkly stippled anterior to vocal sac, and less stippled towards margin of jaw. Lower two-thirds of iris brown, upper third bright copper gold, pale gold border above pupil, less distinct below pupil.

Tympanum unpigmented except for darker patch extending from dorsal edge to centre. Annulus of tympanum pale. Pale lemon yellow wash over upper lip (below stripe), sides and posterior surface of thighs. Bright lemon yellow wash over groin, fades anteriorly. Flanks and posterior surfaces of thighs diffusely mottled with reddish brown colour of dorsum. Dorsal surface of limbs reddish brown (same as dorsum) with diffuse darker mottling. Dorsal surfaces of arms mottled, fingers paler, especially 2nd and 3rd. Outer edge of forearms with darker mottling. Dorsal surface of legs dark with some mottling, especially on posterior edge of thighs where blotches form an uninterrupted line. Belly and ventral surface of limbs pale white, undersurfaces of feet dark brown.

Colour in preservative

Dorsal surfaces much darker than in life – dark slate to chocolate brown – with vertebral and dorsolateral stripes much less apparent. Dark lateral head stripe poorly defined with ground colour discernible beneath; continues past tympanum and fades on side near arms. Yellow wash in groin barely discernible. Undersurfaces pale yellow, hands and feet dark.

Variation

Male body sizes varied only slightly – the smallest was 29 mm and the largest 33 mm (Table 2). The build, proportions and general appearance of male specimens generally agreed with the holotype except for the following (WAM prefixes excluded below). Shape of rostrum varied from sharp and angular (R162614, R162616) to more broadly rounded (R162612). Glandular tissue at angle of jaw similar to holotype for most males, but in R162616, nodules were higher and more prominent, and in R162512, skin was nearly smooth. Nuptial pads ranged from less developed (lighter and less extensive; R162512) to very heavy and extensive (R162537). R162515 possessed slightly rougher pads than other males.

The two female specimens had lengths of 35.5 and 36.5 mm – larger than any of the 10 males. Both females were collected near calling males and were heavily gravid. Other than overall body size there were no obvious differences between males and

Table 2 Summaries of characters and ratios measured for *Litoria staccato*, *L. coplandi* and *L. personata*. Mean±S.D. (range). Sample sizes are for species unless noted. See Table 1A for abbreviations.

Character	*L. staccato* N = 12	*L. coplandi* N = 56	*L. personata* N = 12
SVL	31.4±2.4 (29–36.5)	33.4±4.0 (24.5–43.0)	30.8±2.4 (26.5–33.5)
ILL	13.0±2.1 (10.4–18.4)	13.8±2.1 (8.8–18.0) N = 54	12.3±1.9 (9.5–15.3)
HL	11.3±0.7 (10.4–13.1)	(12.4±1.3) (8.6–15.2)	11.2±0.8 (9.7–12.4)
HW	10.7±0.8 (9.8–12.6)	11.8±1.4 (8.9–14.6)	9.9±0.7 (8.6–11.0)
EN	2.8±0.2 (2.6–3.1)	3.2±0.4 (2.6–4.1)	3.0±0.3 (2.4–3.2)
IO	5.4±0.3 (4.8–6.0)	6.6±0.7 (5.0–8.2)	5.9±0.5 (5.0–6.5)
IN	3.2±0.2 (2.8–3.6)	3.2±0.4 (2.4–4.1)	3.2±0.2 (2.9–3.4)
NM	1.8±0.2 (1.5–2.1) N = 11	2.1±0.3 (1.6–2.7) N = 55	1.7±0.2 (1.5–1.9)
EL	3.2±0.3 (2.8–4.0)	3.7±0.4 (2.9–4.5)	3.3±0.4 (2.6–4.0)
TymL	2.3±0.1 (2.0–2.5)	2.6±0.3 (2.1–3.8)	2.5±0.6 (1.9–3.3)
FL	6.4±0.7 (5.7–7.9)	6.9±0.7 (5.5–8.6)	6.6±0.6 (5.7–8.0)
HandL	7.6±1.2 (6.0–9.6)	8.4±1.3 (5.8–10.3)	7.7±0.6 (6.6–8.5) N = 11
3rdFDW	0.98±0.15 (0.77–1.23) N = 8	1.14±0.23 (0.63–1.81) N = 45	0.93±0.22 (0.60–1.13) N = 8
TL	16.0±1.3 (14.3–18.4)	18.7±2.2 (14.8–24.1)	17.4±1.6 (14.7–20.0)
TarL	8.4±0.6 (7.4–9.7)	9.1±1.1 (7.4–11.4)	9.2±1.0 (7.2–10.6)
FootL	11.9±1.2 (10.8–14.4)	13.3±1.8 (10.4–18.2) N = 55	12.1±1.3 (10.1–13.9)
4thTDW	0.73±0.10 (0.63–0.94) N = 8	0.98±0.25 (0.58–1.68) N = 45	0.72±0.21 (0.48–1.04) N = 8
HW/SVL	0.34±0.01 (0.31–0.36)	0.36±0.01 (0.32–0.36)	0.32±0.01 (0.32–0.36)
HL/HW	1.05±0.03 (1.02–1.10)	1.04±0.05 (0.82–1.16)	1.13±0.04 (1.07–1.21)
EN/IN	0.89±0.04 (0.81–0.95)	0.98±0.08 (0.81–1.16)	0.93±0.06 (0.82–1.04)
EN/IO	0.52±0.02 (0.47–0.56)	0.48±0.04 (0.41–0.57)	0.50±0.04 (0.45–0.57)
TL/SVL	0.51±0.02 (0.46–0.55)	0.56±0.04 (0.45–0.65)	0.57±0.03 (0.49–0.60)
TarL/SVL	0.27±0.01 (0.25–0.29)	0.27±0.02 (0.22–0.33)	0.30±0.02 (0.24–0.33)
TarL/TL	0.52±0.02 (0.49–0.55)	0.49±0.02 (0.44–0.53)	0.53±0.03 (0.48–0.58)

females in morphological characters, but the small number of females prevented further evaluation.

Colouration of males was variable. In addition to the reddish brown of the holotype and paratypes R162537-8, R162612 and R162616, other individuals were bright beige while active in life (R162514 and other uncollected males – Figure 2B). Still others were slate grey (R162512, R162613-5 – Figure 2C). Mottling on the dorsum was also variable – some individuals had darker mottling (e.g., R162612) while others had only faint variegations (e.g., R162514). Collected individuals changed colour from generally vivid while active to more dull and/or mottled the following day, obscuring the diffuse vertebral, dorsolateral and lateral streaks.

The lateral head stripe ranged from relatively demarcated (e.g., R162613) to diffuse grey (e.g., R162514) with borders never sharply defined. In most males, the lateral head stripes did not meet at the tip of the snout, but in one other individual (R162537) they joined, as in the holotype. The paler snout patch outlined by the lateral head stripes and the diffuse posterior bar between the eyes varied in definition from very clear (e.g., R162537) to poorly defined (R162612). Presence of the thin vertebral and wider dorsolateral streaks was highly variable. In some specimens, stripes were relatively solid and dark (e.g., R162613, R162615), in others there was only a slight stripe (R162514), or heavy mottling that obscured stripes (R162612). The border between lateral and ventral regions varied from a smooth transition with little marking (R162514), to a mottled transition zone (R162612, R162614), to a darker stripe (R162613, R162614). Mottling on posterior edge of thighs ranged from diffuse (e.g., R162614-5; as for holotype), to faint uniform stippling (R162612-3), or very faint stippling (R162514).

The two female specimens were similar in colouration – both had the dull reddish brown background colouration seen in several males, with moderate to heavy dark mottling on dorsal surface. Snout patches were less prominent and vertebral, dorsolateral and transverse bars weakly defined. Female R162513 was lighter overall, including paler sides, no stippling on chin and only faint stippling on back of thighs (Figure 2D). Female R162620 was darker, with mottled sides, light stippling on chin and mottling on back of thighs similar to some males.

Advertisement call

The calls of the holotype male (R162611) and a paratype (R162612) were recorded on 30 January 2006 between 7 and 9 pm. The air temperature 1 cm above the males was 28.7°C (R162611) and 26.6°C (R162612), and the temperature of the flowing water about 5 cm below the surface was ~ 29°C for both.

The call of the holotype of *L. staccato* is presented in Figure 3C. It consists of a sequence of rapid, high-pitched, irregularly spaced, short (staccato) notes, followed by a series of softer and more widely spaced notes with occasionally more complex notes (Figure 3C–F). The holotype male called 3.8 times per minute with call duration averaging 6.5 s (maximum – 15 s). Notes in the main call are irregularly spaced, sounding similar to a Morse code signal. There were an average of 25 notes/call and 4.3 notes/s. The notes increased slightly in amplitude during the call (Figure 3C). Each note consisted of a series of 14–19 pulses that increased in amplitude gradually with a sharper decrease, and with dominant frequencies of 2–3 and 4–6 kHz (Figure 3D). Between the main calls, the much less frequent softer calls were delivered in small clusters of typically 3–4 notes (up to six). These notes were made up of 5–8 pulses with dominant frequencies at 2, 3.5 and 5 kHz (Figure 3E). A third type of call was occasionally given among the softer calls that consisted of a rapid, trill-like series of modulated pulses with several peaks (Figure 3F). During the 10 minute recording, the male only began to give these more complex calls in the middle third of the calling sequence. These complex notes were made up of 34–48 pulses, had 4 or 5 peaks in amplitude during the brief (0.15 s) call and had dominant frequencies at 1.5 and 3.5 kHz.

The paratype male (R162612) had very similar call characteristics for the main call, but did not give the soft or complex calls between the main calls. These two individuals were calling on either side of a stream > 5 m apart. In both recordings, other males called simultaneously in response to each other. A gravid female (R162120) was captured within 2 m of R162612.

Breeding choruses

Litoria staccato males called in choruses of 2–6 males in slow-flowing sections of a rocky creek at one site, and around shallow water in crevices or under boulders at another site located on an escarpment. Calling sites included exposed rocks, within crevices and under overhanging vegetation. One male (R162612) was observed calling ~ 10 cm above the water (head facing down and towards the stream) while clinging vertically to a ~ 50 cm boulder at the creek's edge. No males were observed to be within 5 m of each other and males often called from positions on opposite sides of the water body. Calls of males in breeding choruses occurred synchronously.

Embryos

A single clutch of embryos was collected that were either just prior to hatching or just hatched at stages 20–21 with capsules partly decomposed. The clutch was collected from a very small and shallow

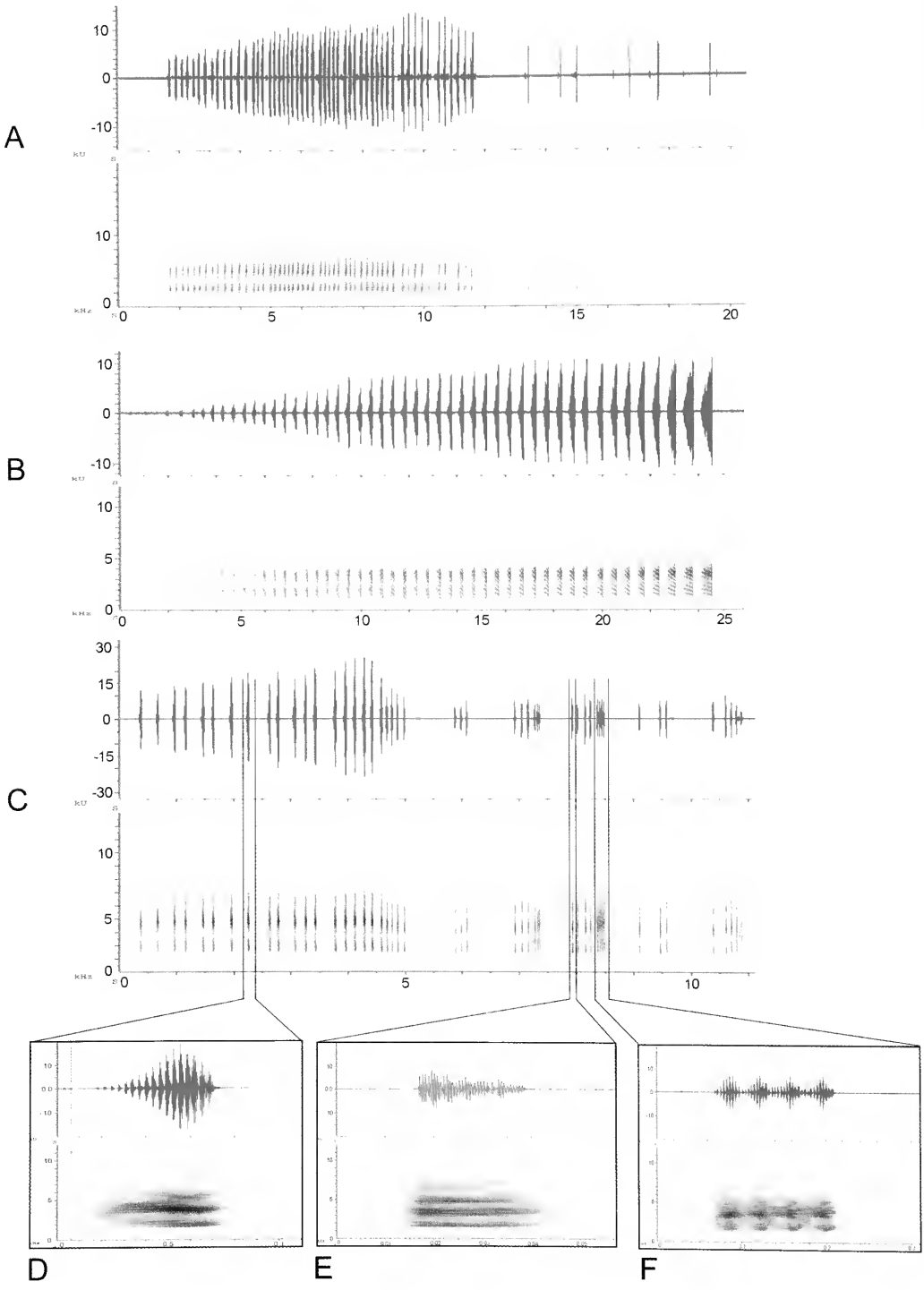


Figure 3 Oscillograms (upper) and sonograms (lower) of male advertisement calls. A) *Litoria meiriana* (WAM R162521); B) *L. coplandi* (uncollected); C) *L. staccato* holotype (WAM R162611); D) *L. staccato* main call; E) *L. staccato* soft call; F) *L. staccato* complex call.

rock pool (70 x 30 cm and 2–3 cm deep) segregated by about two metres from the main creek, most of which was flowing at a reduced water level beneath large boulders. The pool contained leaf litter and tannin-stained water and was on a rock shelf where several calling males and a gravid female were found the previous night. The sample of small tadpoles collected at stages 26–27 was taken from the same pool. The remaining jelly capsules were covered with silt and most were decomposing, but those of six embryos which had died earlier at about stages 13–14 were still intact, and these had a mean external capsule diameter of 3.83 mm (3.54–3.86 mm).

Measurements of embryos are shown in Table 3. Two embryos at stage 20 had shorter gills, darker fins and a less arched dorsal fin than those at stage 21.

Stage 21 (Figure 4A). – Dorsum and tail muscle appear black macroscopically; area above head (lateral view) translucent grey; tail fins dusky grey; snout angular in lateral view; abdomen broad in dorsal view, yolk white; optic bulge discernable but barely pigmented; two pairs well developed external gills with 3–4 upper and 5–6 lower filaments; adhesive organs black and prominent; deep triangular stomodaeum bordered by labial ridges; narial pits visible.

Stage 23 (Figure 4B). – Reached on 10 January; dorsum very dark brown with scattered iridophores over snout, brain, eyes and tail muscle; yolk whitish with network of melanophores dorsolaterally; lateral line organs faintly visible; tail fins dusky grey, melanophores anteriorly across dorsal and partly lateral surface of muscle. Snout broad in dorsal view and rounded in lateral view; eyes well developed, cornea clear; external gills slightly reduced, upper and lower branches of similar length, 4–5 upper and 6–7 lower filaments; adhesive organs broad and flattened; nares perforated, opening anteriorly, quite widely spaced and situated right on tip of snout; labial ridges broader, upper ridge divided; jaw sheaths visible, keratin just visible on edge of upper sheath; operculum open on both sides, short tubular projection on edge of left side – juts outwards (probable early development of spiracle); tail fins well arched, tip broadly rounded; myotomes visible along muscle.

Tadpoles

The largest tadpole grew to a maximum total length of 52.0 mm and body length 17.5 mm (stage 38). Table 3 presents measurements of tadpoles. Tadpoles in captivity were predominantly bottom dwellers and mostly grazed on live algae on rocks and on sediments. Initially water was not aerated and while most tadpoles appeared to grow normally, some died. Aeration was then introduced and the remainder survived, became more agile and grew more steadily. Tadpoles frequently remained in the vicinity of the source of aeration, holding onto rocks with the oral disc. If disturbed, they rapidly darted under rocks or leaves.

Table 4 describes pigmentation development in life. In preservative, all golden, silver and copper iridophores are lost, together with lighter brown pigment, leaving only the darker melanophore patterns visible on the dorsum and tail. The venter

Table 3 Morphometric measurements of tadpoles of *Litoria staccato*, in mm (see Table 1B for abbreviations). Number of specimens: stages 20–21 = 7, 25 = 2, stages 26–29, 32, 38–40 = 1, stage 36 = 3, stage 46 = 2.

Stage	20–21	25	26	27	28	29	32	36	36	36	38	39	40	46
TL	5.72 (5.24–5.98)	12.39, 12.23	20.0	21.5	26.0	29.0	35.0	42.6	40.5	44.0	52.0	49.0	48.3	17.5, 19.0
BL		4.99, 4.99	7.72	8.05	11.1	12.07	13.36	16.74	15.77	16.3	17.5	17.7	17.7	
BD					6.15	6.76	7.24	9.01	8.69			9.98	9.66	
BW					6.72	7.08	7.24	9.98	9.33			10.94	10.78	
EBW					6.64	7.08	7.08	8.05	9.17			10.46	9.82	
BTM					2.29	2.73	3.22	4.18	3.54			5.0	4.83	
BTMW					2.09	2.41	2.57	3.54	3.7			5.15	5.15	
TD					5.49	6.27	6.6	8.05	8.13			9.17	8.69	
DF					1.88	2.09	2.25	2.57	2.65			2.98	3.05	
TM					1.88	2.25	2.25	3.22	3.13			3.7	2.57	
VF					1.72	1.93	2.09	2.25	2.33			2.57	3.05	
IO					3.44	3.78	3.86	4.34	4.34			4.5	4.34	
IN					1.88	2.09	2.09	2.57	2.57			2.57	2.57	
EN					1.93	2.09	2.09	2.57	2.57			2.73	2.73	
N					0.28	0.28	0.32	0.3	0.32			0.32	0.32	
SS					6.44	7.08	8.05	9.41	9.01			10.3	9.98	
SN					1.28	1.28	1.61	2.01	1.61			2.25	1.61	
SE					3.38	3.38	3.7	4.83	4.34			5.15	4.34	
ED					1.36	1.45	1.93	2.09	2.25			2.57	2.57	
ODW					3.19	3.28	3.36	4.18	3.93			4.51	4.67	

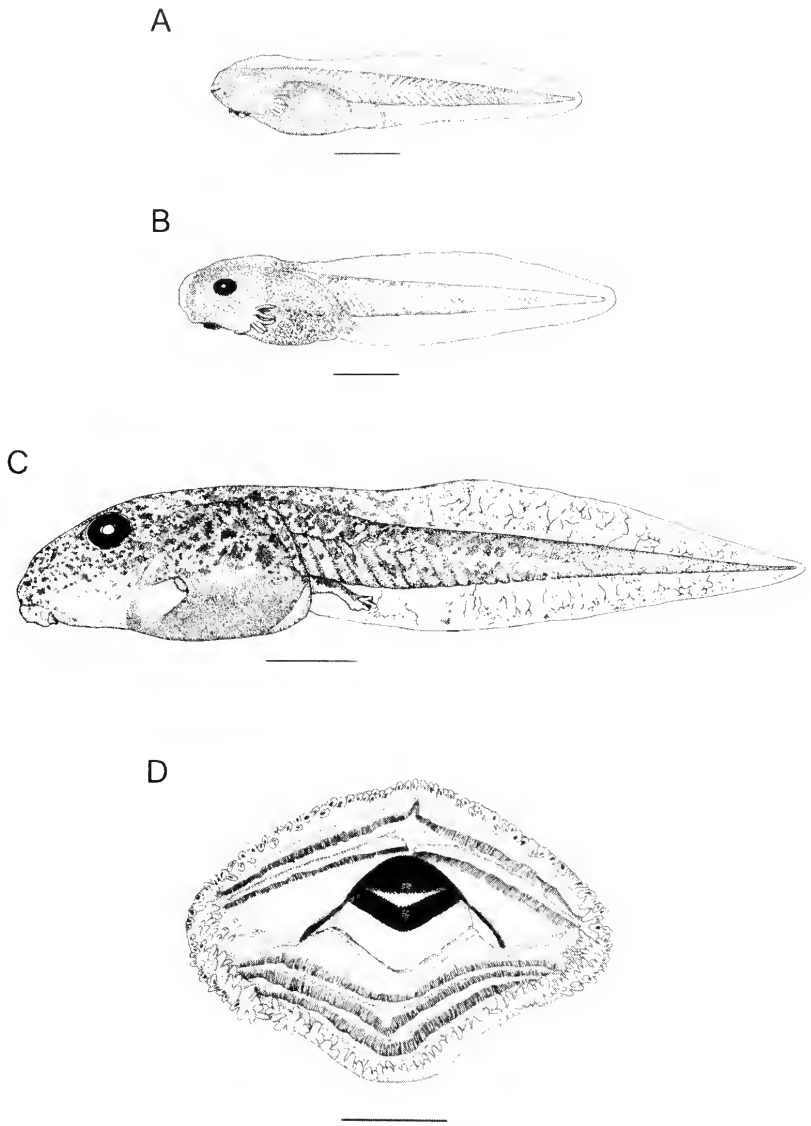


Figure 4 Embryos, tadpole and oral disc of *Litoria staccato*. A) hatchling at stage 20, bar = 1 mm; B) stage 23, bar = 1 mm; C) tadpole at stage 36, bar = 5 mm; D) oral disc, specimen at stage 36, bar = 1 mm.

appears dark grey-blue and the paler snout colour is not visible. Description of the morphological changes during development are presented below.

Stage 25. – Reached by 14 January: body shape cylindrical, similar to Type 2 hylids (Anstis 2002); eyes near lateral; tail fins well arched, tail tip rounded.

Stages 26 and 27 (Figure 4A). – Mostly similar to later stages described below, apart from size and pigmentation changes (see below), in body features, mouthparts and tail features, but the distance from the eyes to the tip of the snout is shorter and the snout is a little narrower in dorsal view.

Stages 32–39. – Medium body size when full grown, as wide as deep across abdomen to about stage 32, slightly wider than deep across abdomen from about stage 36 onwards; snout rounded in dorsal view, gradually becomes broader and slightly more streamlined anterior to eyes from about stage 34 onwards; eyes near lateral, slightly dorsolateral in later stages; nares small, quite widely spaced, open anterolaterally, slightly closer to tip of snout than to eyes; spiracle fairly short, broad, opens dorsoposteriorly below horizontal body axis posterior to midpoint of body; vent tube dextral (type a; Anstis 2002), narrow, and opens

Table 4 Pigmentation of *Litoria staccato* tadpoles at different larval stages (Gosner 1960).

Stage	Dorsum and Eyes	Sides	Venter	Tail
25	Melanophores over dorsum; gold iridophores over most of dorsum (except over darker base of body); some small dark patches over vertebral region.	Gold patch beginning on each side of abdomen at base of body, denser iridophores posterior to gill region.	Mostly transparent, bordered by dense melanophores and gold stippling.	Fins clear, dorsal surface of muscle dark, capped with gold patches spaced along length, lateral surface stippled with melanophores, a few gold iridophores anteriorly.
26-27 (Fig. 5A)	Dorsum mostly uniform golden; areas above brain, around nares, over abdomen and base of body a little darker; iris golden above and below pupil, black at each side and across top.	Gold clusters cover upper half of abdomen, merging down sides to orange-gold, dark background beneath; lower half of abdomen orange-gold, opaque white beneath; orange-gold from gills to eyes, clearer below; distinct pale gold longitudinal patch midway down body along each side of abdomen, just anterior to base of body; another similar but narrower vertical patch just posterior to gill region; pigment lighter anteriorly.	Brilliant orange-gold over abdomen, sparser over gills and clear over buccal region.	fins mostly clear with some dark veins; few gold specks and melanophores on dorsal fin; fine melanophores over muscle anteriorly, gold stippling dorsolaterally over anterior third; lateral surface of muscle mostly unpigmented posteriorly; some gold clusters anteriorly over lower half. Anterior edge of ventral fin bordered with pale gold, gold clusters over vent tube.
32 (Fig. 5B)	Dull golden brown or darker brown with layer of fine copper-gold iridophores over most of head and body, dark longitudinal stripe down each side of vertebral region and dark patch over base of body, indistinct darker mask bridges eyes.	Distinct lateral gold bar present at base of body during at least stages 26-28 now mostly obscured.	Opaque silver-white with copper sheen, clearer below mouth.	Diffuse melanophore clumps over dorsal fin and muscle of tail; few diffuse gold clusters and flecks over muscle and both fins; darker pigmented veins over muscle and fins (some outlined with gold).
36-39 (Fig. 5C,D)	Diffuse melanophore clumps over dorsal fin and muscle of tail; a few diffuse gold clusters and flecks over muscle and both fins; darker pigmented veins over muscle and fins (some outlined with gold); copper stripe extends from middle of base of body just onto dorsal surface of muscl; dense copper-gold covers most of iris.	Mottling covers upper two-thirds of body, denser by stage 38 onwards.	Opaque silver right up to mouth from stage 36.	Darker mottling covers most of tail; numerous pigmented veins, some outlined with gold; gold clusters anteriorly on dorsal fin, copper-gold along anterior edge of ventral fin and over vent tube; darker mottling denser and covers entire tail by stage 38.
42 (Fig. 5E)	Pale triangle on snout anterior to eyes visible, demarcated posteriorly by diffuse darker bar bridging eyes.			

posteriorly, dorsal edge partly unattached behind. Fins moderately arched and taper to somewhat elongate, narrowly rounded tip; dorsal fin begins just onto base of body, initially low then rises more distinctly to highest point anterior to midpoint of tail before tapering; ventral fin less arched.

Oral disc (Figure 4D). – Near ventral in direction in life (anterior medial margin tilts slightly upwards); ventral in preservative. Marginal papillae surround entire disc; anterior marginal papillae mostly in a single row medially to partway down lateral margins, increasing to two offset rows

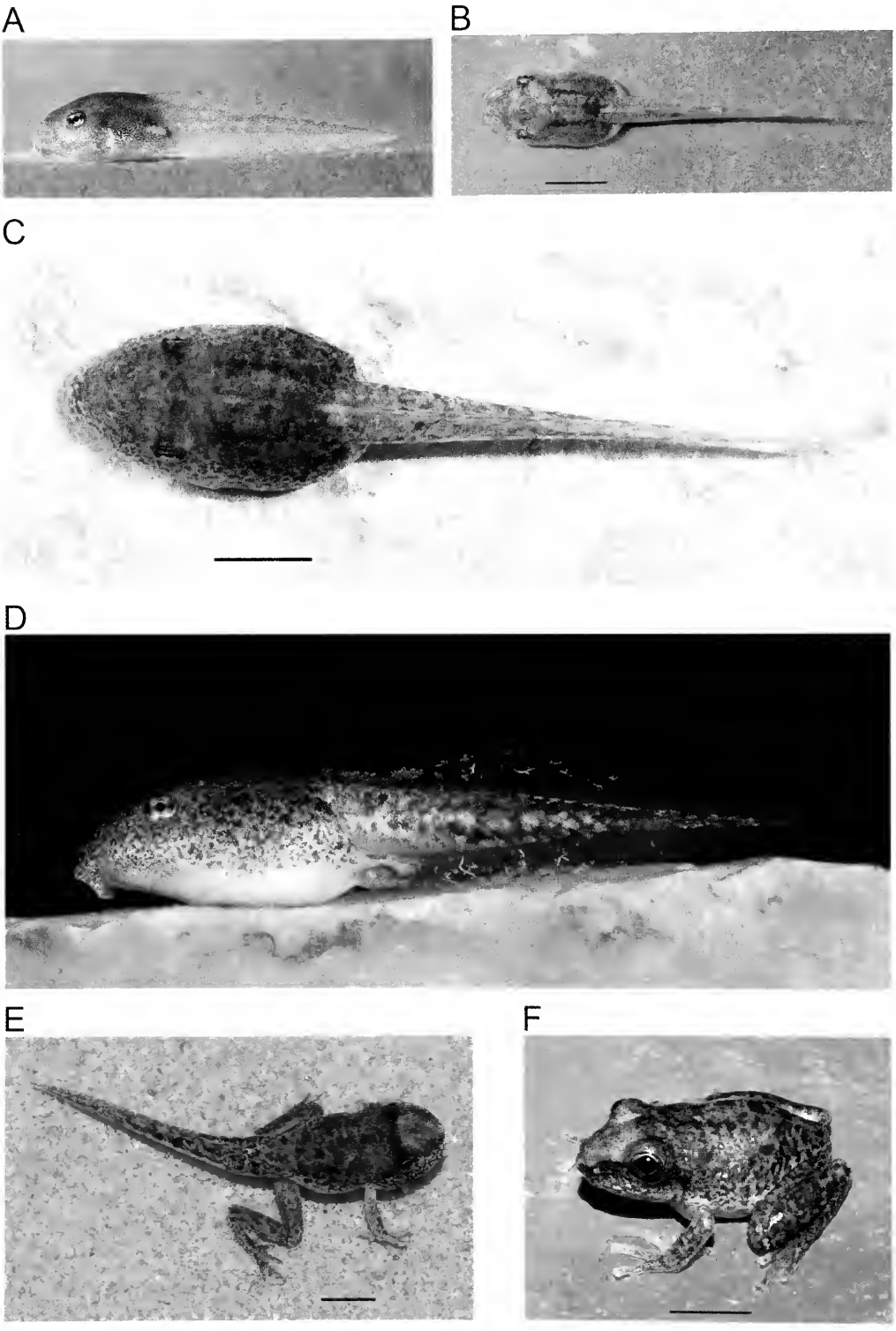


Figure 5 Live tadpoles and metamorph of *Litoria staccato*. A) stage 26 (lateral view); B) stage 32 (dorsal view); C, D) stage 36 (dorsal and lateral views); E) stage 42; F) stage 46. Bar in each photo = 5 mm.

beyond this down each side of anterior half; some have as few as 10–25 medial papillae in a single row across top of disc before two rows begin on each side. Four to six rows of mostly small submarginal papillae at each side of disc; two rows offset slightly longer papillae around posterior margin; may be only one row initially at each side of margin, to up to three rows medially in some. Two anterior and three posterior tooth rows, A^1 continuous, usually with medial pleat (Figure 5B), A^2 has a narrow medial gap, $P^{1,2,3}$ rows continuous, P^3 very slightly shorter. Jaw sheaths medium, quite distinctly serrated and fairly narrowly arched, with long flared lateral processes.

Metamorphosis. – Tadpoles collected at stage 26 on 9 January began to metamorphose on 11 February (33 d later), and hatchlings collected on 9 January first metamorphosed on 20 February (42 d later). Assuming that early development from egg to hatching is likely to take about 3 d in the shallow warm water of the initial pool, minimum larval life span in captivity for the hatchling group was about 45 d. Newly metamorphosed froglets had colouration similar to adults (Figure 5F). Head not quite as proportionately long yet as in adults. Terminal discs and webbing as for adults. Two newly metamorphosed froglets measured 17.5 and 19.0 mm SVL.

Distribution

Currently known from only two locations near "The Grotto", approximately 30 km south of Wyndham, Western Australia (Figure 6). Both locations occur in the rocky southern portion of Parry's Lagoon Nature Reserve east of the Great Northern Highway. The entire collections of *L. coplandi* at the WA Museum (529 specimens), SA Museum (98 specimens), Museum and Art Gallery of the Northern Territory (190 specimens), Queensland Museum (77 specimens) and Australian Museum (151 specimens) were checked for the diagnostic characteristics of *L. staccato*. No specimens of *L. staccato* were detected. This indicates *L. staccato*'s distribution is apparently restricted to the small area where the type series was collected. However, owing to the inaccessibility of the Kimberley region due to the rugged terrain and large areas with no vehicular access, it is likely that the new species will be found elsewhere in the eastern Kimberley, possibly to the northwest of the two known sites and to the east in the Northern Territory where similar habitats occur.

Habitat

Individuals of *L. staccato* were found in two areas with flowing water. The first was a steep rocky ridge with a slow trickle of water running under large boulders where males were calling, and where the eggs and tadpoles were collected (see above). The second area (where the holotype was collected) was a creek that ran down a rocky ridge, about 2–3 km long (Figure 7). Both sources of water came from underground streams that flowed from near the top of ridges.

The vegetation at the rocky ridge sites where *L. staccato* occurs is sparse but dominated by *Triodia wiseana* with *Cochlospermum fraseri, Calytrix exstipulata* and stunted *Erythrophlem chlorostachys*. Along the watercourses where *L. staccato* was calling were *Triodia pungens, Terminalia volucris, Ficus* sp. and occasionally the boab tree *Adansonia gregorii*.

Etymology

Specific name 'staccato' is from the Italian musical term, and refers to the short detached sound of the individual repeated notes of the male advertisement call. It is to be treated as a noun in apposition.

Comparison with other species

1. Adults

In the eastern Kimberley, *L. staccato* may be potentially confused with several species of ground-dwelling *Litoria* which have pointed snouts, such as *L. nasuta, L. pallida, L. inermis* and *L. tornieri*. All of these species have narrow terminal discs on the fingers, whereas *L. staccato* has wider, expanded discs. *Litoria nasuta* has an elongate head with a strongly pointed snout and prominent longitudinal stripes. *Litoria tornieri* has a smooth dorsum, uniform pale body colour and a strongly contrasting dark lateral head stripe that breaks up posterior to the tympanum. *Litoria inermis* has a poorly defined lateral head stripe similar to *L. staccato*, but possesses raised tubercles over the dorsal surface, unlike the smooth skin of *L. staccato*. Although some *L. pallida* also possess a poorly defined lateral head stripe, they can be distinguished by very narrow terminal discs on the fingers, slightly raised tubercles on dorsum, distinctive penetrating call with much longer notes and selection of mostly still water breeding sites. *Litoria wotjulumensis* often breeds along rocky streams, has moderately expanded discs on the fingers and toes and also has a complex call with elements similar to *L. staccato*. However, *L. wotjulumensis* is a much larger species (almost double the length of *L. staccato*), has a more elongate head, possesses a strong, broad lateral head stripe and has fully webbed toes. *Litoria meiriana* also occurs along rocky creeks and rock holes and occurs in the Kimberley and Northern Territory. However, its most obvious difference from *L. staccato* is its much smaller size (~ 20 mm). In addition, *L. meiriana* is dorsoventrally compressed, has tubercular skin and fully webbed toes.

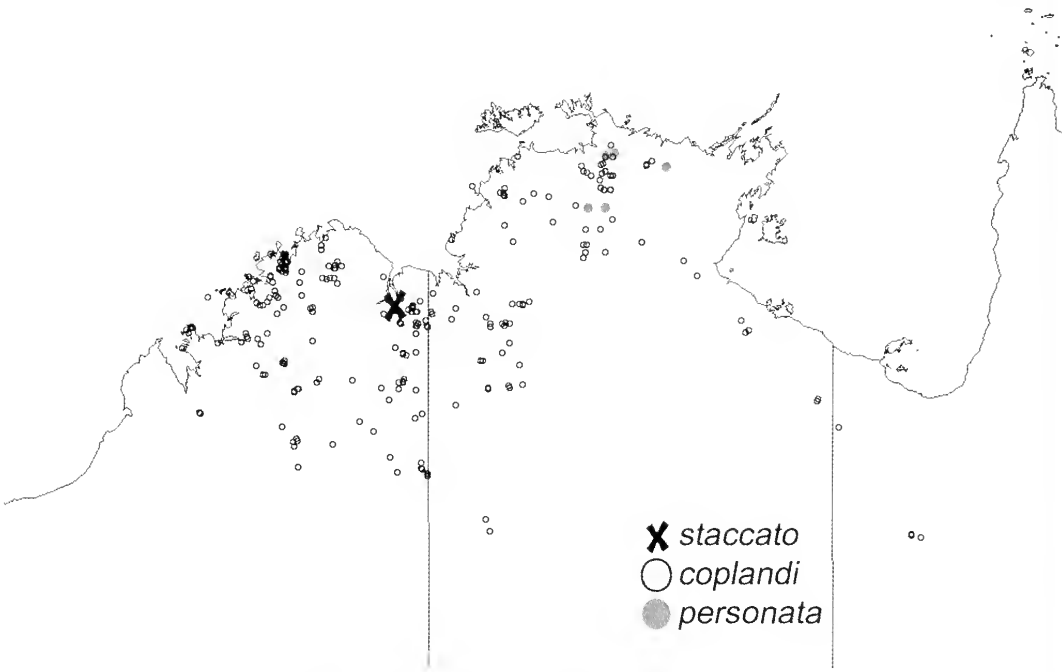


Figure 6 Distribution of *Litoria coplandi*, *L. personata* and *L. staccato* in northern Australia.

The two other rock-dwelling species with similar habits to *L. staccato* and thus most likely to be confused with it, are compared in more detail. Table 2 presents summaries of morphological measurements of *L. staccato*, *L. coplandi* and *L. personata*. *Litoria coplandi* reaches a larger body size, and females of both *L. coplandi* and *L. staccato* are larger than males. The relative head width of *L. coplandi* was wider than the other two species (Table 2). Hind limb proportions of *L. coplandi* and *L. staccato* were similar, but *L. personata* had longer hindlimbs. Thus, *L. staccato* is characterised by a narrower head relative to *L. coplandi* and shorter tibia and tarsus lengths compared to *L. personata*.

A number of other characters further distinguish these three rock-dwelling forms. The most reliable morphological character to distinguish the syntopic *L. staccato* and *L. coplandi* is the extent of webbing between the toes. In *L. staccato* the webbing is reduced, for example the distal two phalanges on the 4th toe are free of webbing and the distal phalanges of the other toes are also free of webbing. In *L. coplandi* the webbing extends to the last phalanx on the 4th toe and to the terminal discs on the remaining toes. The hands and feet of *L. staccato* are more gracile than the more heavily built *L. coplandi*. The webbing between the toes of *L. personata* is only slightly more extensive than *L. staccato* and much reduced relative to *L. coplandi*. Another consistent character among the three species is the glandular tissue at the angle of the jaw. This tissue is pronounced and raised into several discrete nodules in *L. coplandi*, much reduced in *L. staccato* (fewer and lower in profile) and absent in *L. personata*.

All three rock-dwelling hylids possess differences in dorsal colour and patterns that can be used to distinguish them, but these are individually variable and some are not retained or less evident in preservative. Ground colour of *L. coplandi* and *L. personata* ranges from light to medium brown, whereas *L. staccato* ranges from beige to slate grey to reddish brown (the majority of individuals). *Litoria coplandi* and *L. personata* have a relatively uniform dorsal colour. In contrast, many *L. staccato* individuals have more extensive mottling and possess variably expressed vertebral, dorsolateral and lateral stripes. The presence and prominence of a lateral head stripe is another way to separate them. *Litoria personata* has a strong, clearly defined lateral head stripe, *L. staccato* has a less prominent stripe with diffuse borders and *L. coplandi* lacks a lateral head stripe (unique in the *L. lesueuri* complex; Tyler 1968a; Barker *et al.* 1995).

2. Advertisement call

For the purposes of comparison, we present the calls of two sympatric rock-dwelling hylids for which no sonograms have been published, *L. coplandi* and *L. meiriana* (Figure 3A,B). Both males called within 5 cm of the edge of exposed rock

Figure 7 Type locality of *Litoria staccato* near Wyndham, Western Australia.

pools. The temperature 1 cm above the calling *L. meiriana* was 28.2°C with a water temperature of 32.1°C; the *L. coplandi* male was recorded shortly after, and within 50 m of the *L. meiriana* male.

The call of *L. meiriana* is most similar to *L. staccato* owing to the notes of the main call being irregularly spaced (similar to Morse code). However, *L. meiriana* has a much higher-pitched call (dominant frequencies of 2–3 and 4–6 kHz) and the softer notes between main calls occur singly (Figure 3A), unlike in *L. staccato* (Figure 3C). The call of *L. coplandi* (Figure 3B) is easily distinguished by a combination of regularly-spaced notes, longer duration call (> 20 s), main call begins very softly then increases steadily in amplitude, dominant frequencies of 1–2 and 3–4 kHz and single softer notes between main calls (as in *L. meiriana*).

The call of *L. wotjulumensis* (not shown or analyzed) is highly distinctive and very complex (*personal observations*). The call contains loud, sustained sequences of calls that abruptly double in rate. The sustained calls can last for over 30 s and are usually followed by a series of complex trills, similar to the complex trill-like notes of *L. staccato*, but given more frequently. Owing to the few males that were recorded, our comparative results are best considered preliminary. More detailed sound analyses of more individuals and species is likely to yield additional differences between species and also provide estimates of variation within species. The calls of all species discussed above may be heard on www.museum.wa.gov.au/frogwatch.

3. Eggs and tadpoles

The remains of the egg mass collected indicate that eggs may be laid in fairly loose clumps attached to substrate rock. The eggs of *L. coplandi* also have been found laid on the floor of shallow rock pools singly or in small clumps (Tyler *et al.* 1983).

The tadpoles of *L. staccato* are distinguishable from *L. coplandi* as early as at stage 25, when the mouthparts are complete, as *L. coplandi* tadpoles have two rows of continuous anterior papillae and *L. staccato* have only a single continuous row across part or all of the anterior margin. In addition, fully grown *L. coplandi* tadpoles have a more distinctly streamlined body form and a wider oral disc that appears to be slightly more suctorial than that of *L. staccato*. Of the other species of hylid tadpoles which are found in stream pools in the escarpment areas of the region, *L. staccato* have a generally similar body size and shape to those of *L. inermis* and *L. wotjulumensis* tadpoles, although they become slightly more streamlined anteriorly than *L. inermis* in later stages. Both *L. inermis*, *L. wotjulumensis* and all other known ground hylid species (with the exception of *L. coplandi*) in the Kimberley region of northern Australia have a narrow medial gap in the anterior papillae.

Remarks

New species of frogs are still being described in Australia, especially in the northern tropics and the eastern margin of the continent, where they are most diverse. Recent descriptions include the discovery of a highly distinctive stream-dwelling tree frog in north Queensland, *L. andirrmalin* (McDonald 1997), and a cryptic species of *Uperoleia* near Darwin, *U. daviesae* (Young *et al.* 2005). Genetic techniques and analysis of calls are resulting in further cryptic species being uncovered in frogs previously considered to be one species (e.g., *L. lesueuri*, which has now been split into three species, Donnellan and Mahoney 2004; see also Donnellan *et al.* 1983; Hoskin 2004).

The recent discovery of *L. staccato* highlights the possibility that more undescribed species of frogs may occur in the Kimberley region. Other than the sealed Great Northern Highway and the unsealed Gibb River Road, only the Mitchell Plateau has been reasonably sampled for frogs. Many surveys to other regions (e.g., Kendrick and Rolfe 1991) were designed to collect surface-active terrestrial

vertebrates but did not specifically target frogs and did not involve night searches when breeding males are easily located by their calls. Future wet season frog surveys involving night work, recording of male calls and taking tissue samples for molecular analysis are likely to yield more undescribed species in the Kimberley Region.

Little is known of *L. staccato*. Breeding choruses occurred along rocky creeks up ridges or beside seeps running down rock faces. In the area near The Grotto where the type series was collected, several other species were calling. Calling from ponds on the flats between the ridges were the myobatrachids *Crinia bilingua*, *Opisthodon ornatus*, *Notaden melanoscaphus* and *Uperoleia lithomoda*, and the hylids *Cyclorana australis*, *C. longipes*, *L. bicolor*, *L. pallida* and *L. nasuta*. Calling along large flowing rocky creeks at the base of the ridges were *U. borealis* and *L. wotjulumensis*. Further up the ridge, calling males of *U. borealis*, *Limnodynastes lignarius*, *Litoria coplandi* and *L. staccato* occurred along small flowing rocky creeks. Near the top of the ridge, only *Limnodynastes lignarius* and *Litoria staccato* occurred. The reduced webbing on the feet of *L. staccato* (compared to *L. coplandi*) may indicate they are somewhat less aquatic, consistent with their distribution further up the two ridges than *L. coplandi*, where there is less water in creeks. Much more work is needed to gain a better understanding of the habits and distribution of *L. staccato* in the Kimberley region and possibly in adjacent parts of the Northern Territory.

ACKNOWLEDGEMENTS

We thank CALM "toadbusters" J. Francis and C. Mills for assistance in the field during the discovery and collection of the type series. G. Graham, G. McKae and the staff of CALM-Kununurra provided accommodation and logistical support for our surveys during the 2005–2006 wet season. We thank C. Stevenson (Western Australian Museum) for the drawings of the adults and the distribution map and J. Francis for the photograph of a calling male *L. staccato* (Figure 2C). Technical advice and loan of equipment for audio recordings and analysis were provided by J. D. Roberts (University of Western Australia) and C. Gerhardt (University of Missouri). We thank P. Horner (Museum and Art Gallery of the Northern Territory), P. Couper (Queensland Museum) and M. Hutchinson (South Australian Museum) for loan of specimens, and S. Reynolds (Charles Darwin University) and P. Oliver (Adelaide University) for searching through the *L. coplandi* collections for specimens of the new species. This work was made possible through the Western Australian Museum's Alcoa Frog Watch programme funded by Alcoa of Australia. This paper is dedicated to the volunteer "toadbusters" of the Kununurra community.

REFERENCES

Anstis, M. (2002). *Tadpoles of south-eastern Australia: a guide with keys*. Reed New Holland, Sydney, NSW.

Anstis, M. and Tyler, M. J. (2005). Breeding biology of *Litoria microbelos* (Cogger) (Anura: Hylidae). *Transactions of the Royal Society of South Australia* **129**: 43–48.

Barker, J., Grigg, G. C. and Tyler, M. J. (1995). *A Field Guide to Australian Frogs*. Surrey Beatty & Sons, Chipping Norton, NSW.

Charif, R. A., Clark, C. W. and Fristrup, K. M. (2004). *Raven 1.2 User's Manual*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Donnellan, S., Adams, M., Hutchinson, M. and Baverstock, P. R. (1993). The identification of cryptic species in the Australian herpetofauna: a high research priority (pp. 121–125). *In* Lunney, D. and Ayers, D. (eds.) *Herpetology in Australia: a diverse discipline*. Surrey Beatty & Sons, Chipping Norton, NSW, Australia.

Donnellan, S. C. and Mahoney, M. J. (2004). Allozyme, chromosomal and morphological variability in the *Litoria lesueuri* species group (Anura: Hylidae), including a description of a new species. *Australian Journal of Zoology* **52**:1–28.

Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**:183–190.

Hoskin, C. J. (2004). Australian microhylid frogs (*Cophixalus* and *Austrochaperina*): phylogeny, taxonomy, calls, distributions and breeding biology. *Australian Journal of Zoology* 52:237–269.

Kendrick, P. G. and Rolfe, J. K. (1991). The reptiles and amphibians of Kimberley rainforests (pp. 347–359). *In* McKenzie, N. L., Johnston, R. B. and Kendrick, P. G. (eds.) *Kimberly Rainforests of Australia*. Surrey Beatty & Sons, Chipping Norton, NSW.

McDonald, K. R. (1997). A new stream-dwelling *Litoria* from the Melville Range, Queensland, Australia. *Memoirs of the Queensland Museum* **42**:307–309.

Tyler, M. J. (1968a). A taxonomic study of hylid frogs of the *Hyla lesueuri* complex occurring in north-western Australia. *Records of the South Australian Museum* **15**:711–727.

Tyler, M. J. (1968b). Papuan hylid frogs of the genus *Hyla*. *Zoologishce Verhhandelingen* **96**:1–203.

Tyler, M. J. and Davies, M. (1978). Species groups within the Australopapuan hylid frog genus *Litoria* Tschudi. *Australian Journal of Zoology* **63** (supplement):1–47.

Tyler, M. J., Davies, M. and Martin, A. A. (1978). A new species of hylid frog from the Northern Territory. *Transactions of the Royal Society of South Australia* **102**:151–157.

Tyler, M. J., Crook, G. A. and Davies, M. (1983). Reproductive biology of the frogs of the Magela Creek system, Northern Territory. *Records of the South Australian Museum* **18**: 415–440.

Young, J. E., Tyler, M. J. and Kent, S. A. (2005). Diminutive new species of *Uperoleia* Grey (Anura: Myobatrachidae) from the vicinity of Darwin, Northern Territory, Australia. *Journal of Herpetology* **39**: 603–609.

Manuscript received 25 July 2006; accepted 18 October 2006

APPENDIX

Comparative material examined.

Abbreviations: SAM – South Australian Museum; NT – Museum and Art Gallery of the Northern Territory; QM – Queensland Museum; note specimen numbers without one of these prefixes are from the Western Australian Museum.

Litoria coplandi

Males – WAM R103060, R108792, R110746, R114039, R114090, R119091, R114092, R129193, R137838, R137384, R137385, R140357, R140362, R152951, R162520, R162523, R162524, R162535, R162536, R162539, R162547, R162548, R162549, R162950, R162581, R162596, R162597, R162602, R162603, R162609, R162610, QM J54933, QM J56592, QM J56588, QM J56595, QM J56580.

Females – R97942, R114088, R127332, R137382, R137389, R138879, R138883, R138894, R140351, R140352, R140361, R140369, QM J53809, QM J56584, QM J56596.

Juveniles (sex unknown) – R95599, R129194, R95509, R87922.

Litoria personata

Males – NT R16886, NT R18794, NT R18795, NT R19807, NT R19809, NT R20466, SAM R16773, SAM R16774.

Females – NT R20467, NT R20468, SAM R16831, SAM R16832.

Juvenile – SAM R16829.

Note added in proof.

Field trips in 2006-2007 have recorded *L. staccato* from the Mitchell Plateau and Prince Regent Nature Reserve, greatly extending its distribution.

Records of the Western Australian Museum **23**: 259–271 (2007).

Direct development in two Myobatrachid Frogs, *Arenophryne rotunda* Tyler and *Myobatrachus gouldii* Gray, from Western Australia

Marion Anstis[1], J. Dale Roberts[2], and Ronald Altig[3]

[1] 26 Wideview Rd., Berowra Heights, NSW 2082, Australia. Email: frogpole@tpg.com.au

[2] School of Animal Biology (M092), University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009 Australia

[3] Department of Biological Sciences, Mississippi State University, Mississippi State, MS 39762 USA

Abstract – The closely related Western Australian myobatrachid frogs *Arenophryne rotunda* and *Myobatrachus gouldii* deposit eggs in burrows that are dug by the adults in moist sand. Embryonic development requires up to two months and is completed entirely within the jelly capsule. The developmental stages of these two taxa are described and compared with those of the South American direct developing leptodactylid frog *Eleutherodactylus coqui*.

Key words: Australia, direct development, embryo, endotrophic, myobatrachid

INTRODUCTION

The frogs *Arenophryne rotunda* and *Myobatrachus gouldii* (Myobatrachidae) are widely distributed in semi-arid and arid regions of southwestern Australia (Tyler *et al.* 2000). Both species are forwards burrowers that oviposit deep underground in moist sand where embryos undergo direct development, an endotrophic breeding mode in which all embryonic development through to a froglet takes place within the jelly layers of the egg (Altig and Johnson 1989). *Arenophryne rotunda* calls from July-November (austral winter to spring). Pairs of males and gravid females not in amplexus have been found together in November at a mean depth of 45 cm, and in February and April (late summer to autumn) at mean depths of 75–78 cm, but eggs were only found in April (Roberts 1984). *Myobatrachus gouldii* calls from September-February (spring to late summer); a male and female burrow together, not in amplexus, into deep, moist sand where they appear to remain together until autumn when they deposit eggs at depths of 80–115 cm (Roberts 1981, 1984). Tyler's (1976a) suggestion of a close relationship between these two species and with *Metacrinia* was supported by Maxson and Roberts (1985), Read *et al.* (2001) and the recent analysis by Frost *et al.* (2006).

Direct development in amphibians has evolved in at least seventeen genera from nine families of anurans worldwide (Thibaudeau and Altig 1999). Although the life histories of a number of these species have been described, especially for the genus *Eleutherodactylus* (e.g. Gitlin 1944; Jameson 1950; Wake 1978; Townsend and Stewart 1985), there are no available descriptions of the Australian species which include the myobatrachid genera *Arenophryne*, *Myobatrachus* and *Metacrinia* and the microhylid genera *Austrochaperina* and *Cophixalus*.

The South American leptodactylid genus *Eleutherodactylus* consists of several direct developing species and the field staging system developed for *E. coqui* by Townsend and Stewart (1985) is the most comprehensive system available for this breeding mode. We describe some preserved embryonic material in the Western Australian Museum of *A. rotunda* and *M. gouldii* and compare them to *E. coqui* (see Table 3 and Discussion). Brief comparisons to Australian direct developing microhylids and also to species from other Australian endotrophic guilds including the nidicolous, paraviviparous and exoviviparous species are made where relevant. These are not direct developers because they have a hatched tadpole stage (*sensu* Altig and Johnston 1989), but have some similar characteristics to *A. rotunda* and *M. gouldii* in early stages.

MATERIALS AND METHODS

Fifteen embryos of *A. rotunda* from four clutches collected near Shark Bay, WA and reared in the laboratory in April 1981 by J. D. Roberts, were preserved at irregular intervals in Tyler's fixative (Tyler 1962) and transferred to 70% ethanol when accessioned into the West Australian Museum: WAM R97047-50, 97053, 97057, R97059-60 (see

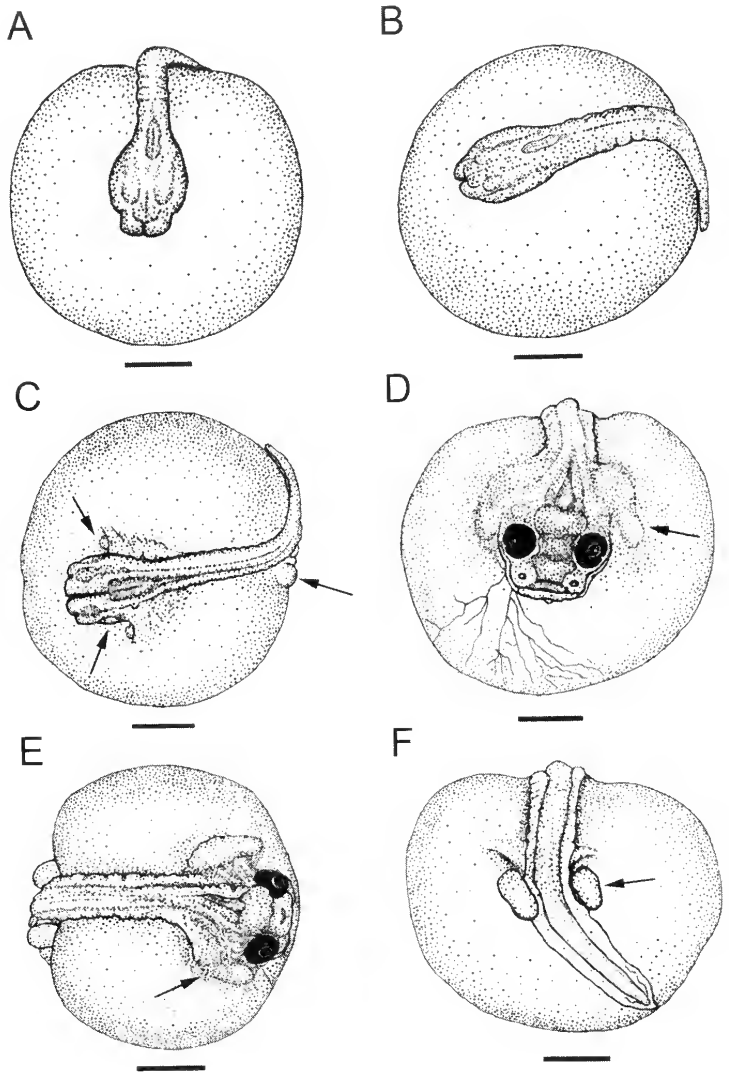


Figure 1 Stages 3, 4 and 6 (Townsend and Stewart, 1985) of *Arenophryne rotunda*. A and B = stage 3, anterior and lateral view; C = stage 4, dorsal view; D, E and F = stage 6, anterior, dorsal and posterior views. Scale bar represents 1 mm. Arrows indicate features highlighted in bold in Table 1.

Appendix 1). Nine embryos up to stage 13 of Townsend and Stewart (T&S; 1985) from one clutch of *M. gouldii* were collected 15 km north-east of Perth, WA, then reared and preserved at irregular intervals: WAM R97036-40. Six individuals just prior to hatching and recently hatched from four marked nests in the field were preserved after being excavated in April 1982: WAM R97041-42, 97044-45 (see Appendix 2). All embryos were reared in total darkness at ambient room temperatures in the laboratory which were lowered slightly (approximately 17–20°C) to better simulate cooling conditions at the nest sites in the field. Measurements were taken with an ocular micrometer attached to a Wild M5 stereoscopic microscope and drawings were prepared with the aid of a camera lucida. The photograph (Figure 4F) was taken with a Nikon D70 digital SLR camera and 60 mm micro lens. Embryos were staged using the system of Townsend and Stewart (1985) which was devised for the direct developing leptodactylid *E. coqui*, with additional references to toe development based on the staging table for aquatic larvae of Gosner (1960). For the sake of completeness, descriptive observations on egg clutches provided for *A. rotunda* and *M. gouldii* by

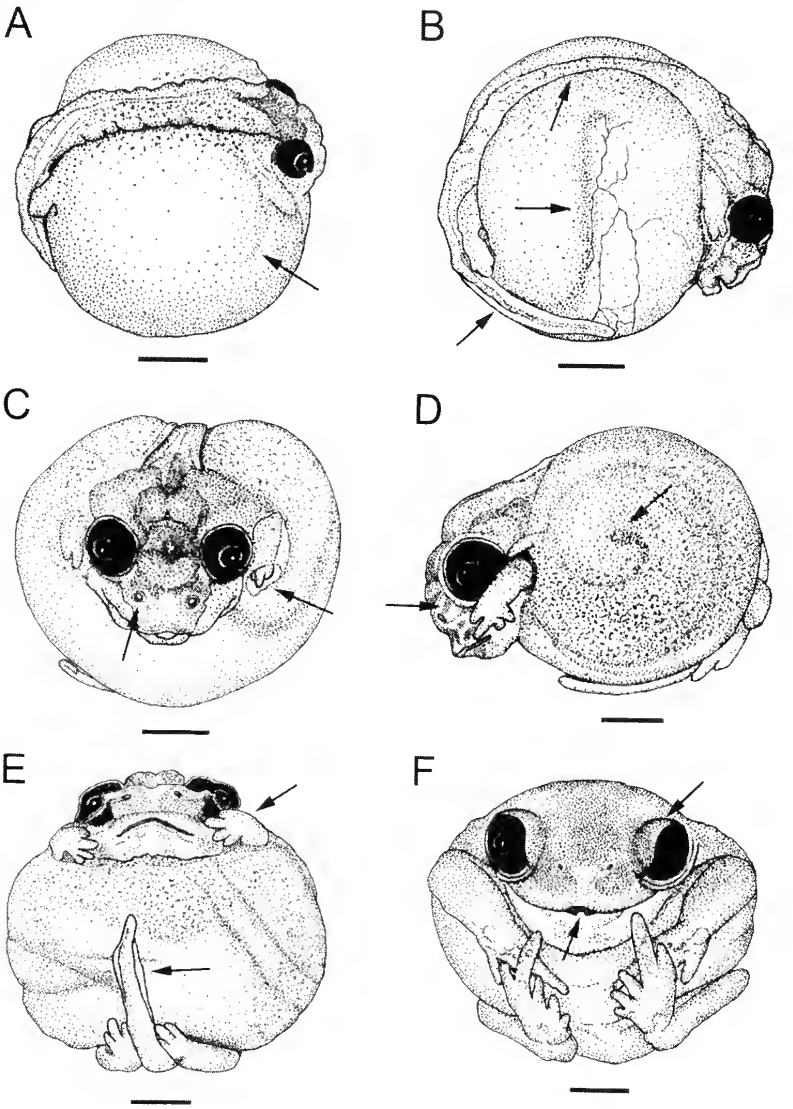


Figure 2 Stages 6, 7, 9, and 15 (Townsend and Stewart, 1985) of *Arenophryne rotunda*. A = stage 6, dorsolateral view; B and C = stage 7, lateral and anterior views; D and E = stage 9, lateral and ventral views; and F = stage 15, just prior to hatching, ventral view. Scale bar represents 1 mm. Arrows indicate features highlighted in bold in Table 1.

Roberts (1984 and 1981, respectively) are summarised prior to the descriptions for each species, with additional notes on development (Roberts, unpubl. data). Embryos in stages 1, 2, 3–7, 9–11, 13 and 15 are described and most stages are illustrated (Figures 1–4). Brief observations were made on live embryos during early cell division. The partial deterioration of the youngest preserved embryos of *A. rotunda* (stages 1 and 2), and specimens of *M. gouldii* at stages 11 and 13, limited their descriptions.

Results

The two species have various morphological characteristics in common. Both have a generally similar parallel progression through the developmental stages described in Tables 1 and 2. Measurements of embryos for each species are given in the Appendices and Table 3 summarises key differences between the Australian species and *E. coqui*.

Development of *Arenophryne rotunda*

Clutch sizes of fertilised eggs ranged from 4–11 (mean 7, n = 5). Ovarian development commences in spring (late August), but ovum maturation is not completed until late summer. Three females collected in February 1981 contained 8, 8 and 4 pale

Table 1 Development of *Arenophryne rotunda*. T&S = Townsend and Stewart (1985) stages. Figure numbers in parenthesis. Features indicated by arrows in Figures 1 and 2 are highlighted in bold.

T&S	Head and Body	Tail	Limbs	Eyes	Mouth	Pigmentation
3 (Fig. 1A,B)	- head region small and narrow - narrow neural tube raised and groove closed, myotomes indistinct - yolk sac large and round - slight gill arch bulges - small indent in yolk in region of vent	- tail bud short, narrow, adpressed around base of yolk, tip pointed - dorsal fin a shallow ridge	- none	- optic bulges small, indistinct, unpigmented	- stomodaeum a small central pit in narrow crevice beneath top of snout, broad anterior bulge on either side	- unpigmented
4 (Fig. 1C)	- head region slightly broader, adpressed against yolk - narrow cleft separates indistinct narial regions - **no external gills** or adhesive organs - small vent opening - some blood vessels present	- tail bud narrow, longer, wraps over limb buds and vent to one side around yolk - fin ridges just visible	- **small round external hind limb buds** - **small round forelimb buds** beneath fold of operculum that extends from side of head across to yolk	- upper crescent of optic bulges slightly pigmented	- mouth slit open, about one-third head width	- unpigmented
6 (Fig. 1D-F, 2A)	- head broader, slightly raised above yolk; snout short, broad, blunt - vertebral region broader and thicker - no spiracle develops - nares perforated - blood vessels anteriorly over yolk - early gut development begins – **faint arc in yolk anteriorly**	- fins low, slightly vascular near tip - muscle narrow - tip rounded to acuminate	- **forelimb buds longer, alongside head beneath operculum** - hind limb buds longer, as in Gosner stages 30-31, slight knee constrictions and foot paddle	- mostly pigmented, slight choroid fissure in lower half of iris - eye diameter 0.7 mm	- mouth opening about one-third head width - upper and lower jaws further developed	- some fine melanophores stippled over brain, vertebral region and onto yolk - tail unpigmented

7 (Fig. 2B-D)	- body broadens slightly - **vertebral region flatter and recessed within yolk** (Fig. 2C) - no external gills develop - internal flap inside naris - **first gut wall in each side of yolk**; vitelline blood vessels increased - groove down either side of vertebral region	- **tail longer, tightly adpressed around yolk**, extends to about midway around yolk - fins low	- limbs lengthen, slight indent on each side of foot paddle as for Gosner stage 33 - **left forelimb partly protrudes through operculum** (Fig. 2C)	- diameter noticeably increased to 1.14 mm - fully pigmented, choroid fissure closed	- mouth widens further	- melanophores denser over head, vertebral region and down sides of yolk
9 (Fig. 2D, E)	- head well defined and prominent, snout broadly truncate, chin raised above yolk - vertebral myotomes more defined - nares oval, diameter 0.1 mm, directed anteroventrally, **internal flap more distinct; lacrimal groove from naris to eye** (Fig. 2D) - vent bordered by narrow rim - **thick, spiral yolk-filled coil in gut**	- **tail remains narrow**, extends two-thirds around yolk - tip narrow	- **forelimbs completely erupted** through operculum - hind limbs longer with distinct knee joints, toes with 5 digits discernable, as for Gosner stage 36	- eyes lateral, prominent, diameter 1.3 mm	- mouth about half head width - small, conical structure begins to project upwards on inside centre of lower lip, corresponding notch above in upper lip	- entire dorsum and sides of yolk uniform light brown - tail unpigmented
15 (Fig. 2F)	- head and body fully defined - intestinal coil thick, yolk-filled, partly visible through epidermis, not yet differentiated into digestive system of adult	- fully resorbed	- limbs fully developed, forearms more robust than hindlimbs	- eyes large, **eyelids and nictitating membrane formed**	- mouth extends to below each eye - **conical structure fully formed**, fits into notch in upper lip (now deeper posteriorly) when mouth closes	- entire dorsum uniform brown, including limbs (above and beneath)

Table 2 Development of *Myobatrachus gouldii*. T&S = Townsend and Stewart (1985) stages. Figure numbers in parenthesis. Features indicated by arrows in Figures 1 and 2 are highlighted in bold.

T&S	Head and Body	Tail	Limbs	Eyes	Mouth	Pigmentation
5 (Fig. 3A-C)	- head and snout fairly broad, adpressed against yolk - vertebral region narrow, raised above yolk - yolk large and round, **some blood vessels anteriorly** - gill arch bulges, no external gills - no adhesive organs - nares perforated, widely spaced - small medial **vent beneath base of tail**, rim around opening	- **well advanced, extends almost halfway around yolk** - fins low at base of body, broaden towards tip - **tip broadly rounded, vascular**	- **small, round to ovoid external hind limb buds** - **small round forelimb buds mostly covered by opercular fold** extending from each side of head (Fig. 3B)	- iris mostly pigmented around outer third - narrow choroid fissure	- mouth slit open, one-third head width	- few fine melanophores scattered over brain and vertebral region to base of body
6 (Fig. 3D,E)	- head larger, broader, chin slightly raised above yolk - snout short, broad, truncate - vertebral region broad, recessed into yolk - nares deeper, no spiracle - yolk slightly expanded, **first gut coil begins** - vitelline blood vessels increased	- tail as for stage 5 in single specimen observed	- **hind limb buds broad, longer, as in Gosner stage 30** - **forelimb buds longer, beneath operculum** alongside head	- almost fully pigmented - choroid fissure narrow - diameter 0.8 mm	- mouth opening slightly more than one-third head width - upper and lower jaws defined	- dorsal pigment increased over head, vertebral region and partly onto yolk - tail unpigmented
9 (Fig. 3F, 4A)	- head broad, frog-like - snout short, broad and truncate, directed anteroventrally - body slightly broader - vertebral region broader, slightly raised, shallow groove down either side and down centre, **myotomes visible** (Fig. 3F) - nares oval, anterior, rim present, internal flap extends downwards - thick spiral intestinal coil	- tail full length, extends to beneath head - fins broader towards tip - muscle broad at base, flat against body, begins to taper from mid-length to tip	- hind limbs adpressed ventrally around yolk, **5 toe digits as for Gosner stage 35** - **forelimbs longer, alongside head**, fingers visible beneath operculum (Fig. 4A)	- eyes lateral - choroid fissure closed - diameter 1.2 mm	- small, conical structure (visible when mouth opened), begins to project upwards from inside centre of lower lip; small corresponding notch above in upper lip	- dorsum uniform brown over brain, vertebral region; less dense over yolk to midway down sides of body - limbs partly pigmented - tail unpigmented

10 (Fig. 4B,C)	- head broad, well defined, more frog-like - diameter of nares 0.16 mm, distinct lacrimal groove from each naris to each eye - **thick spiral coil in gut, visible through epidermis**	- tail extends to forearm in one specimen - muscle slightly translucent down centre of posterior half	- hind limbs longer, toes as for Gosner stage 37, shorter than fingers - **both forearms completely erupted through skin, robust**	- eyes prominent - diameter 1.2 mm	- mouth opening about half head width - **conical structure further developed**, nonkeratinised	- entire dorsum uniform brown, darker over head and vertebral region - sides of body lightly pigmented to partway across venter - limbs lightly pigmented, mainly over upper half - tail unpigmented
11	- specimen dead prior to preservation, misshapen - vertebral myotomes quite distinct	- tail almost full length of body	- toes as for Gosner stage 38, to about half length at hatching			- dorsum uniform brown, lighter brown over limbs and sides - mid-ventral region remains unpigmented
13 (Fig. 4D)	- head broadens further - snout very short and blunt - body appears fully formed, but dead prior to preservation, partly misshapen	- tail regresses to about midway around side of body - muscular ridges clearly defined - tip still broadly rounded	- limbs fully developed, similar to about Gosner stage 43 - subarticular tubercles present			- dorsum uniform dark brown, slightly lighter over limbs and sides of body - throat and chest stippled with brown ventrally - creamy yellow of yolk visible ventrally - tail unpigmented but for a few dark specks anteriorly over muscle
15 (Fig. 4E, F)	- head and body fully defined as a miniature of adult -intestinal coil still yolk-filled, partly visible through epidermis, not yet differentiated into digestive system of adult - nares very small, diameter 0.08 mm, opening further obscured by internal flap	- tail fully resorbed	- limbs fully developed - forearms more robust than hindlimbs	- like those of adult, **eyelid, nictitating membrane present**	- mouth extends to below each eye, tongue visible - **conical structure fits into notch in upper lip** (now deeper posteriorly) when mouth closes	- entire dorsum and limbs uniform dark brown - entire venter and undersurface of limbs stippled brown, darker over throat - soles of feet darker

Table 3 Differences between available preserved stages of *A. rotunda* and *M. gouldii* and those of similar live stages for *E. coqui*. As no observations of behaviour or ECD (endolymphatic calcium deposits, visible in life) were available for the Australian genera, these are not included here for *E. coqui*. Stages prior to stage 4 and features which are the same for each are excluded. T&S = Townsend and Stewart stages (1985).

T&S	*Eleutherodactylus*	*Arenophryne* and *Myobatrachus*
4	• eye bulges distinct • gill arches present, but no gills present • tail bud first apparent	• eye bulges discernable • slight gill arches • tail bud elongates enough to bend around yolk to one side
5	• forelimbs round to ovoid, external • eyes prominent, unpigmented • gill buds first appear from gill arches, gill circulation • tail bud elongates enough to bend, small thin fin	• forelimb buds beneath operculum • eyes partly pigmented • indistinct gill arches, no gills • tail long (especially *Myobatrachus*), wraps around yolk, fins well developed and vascular (*Myobatrachus*),
6	• forelimbs develop externally • eye distinct from rest of head, pupil clear • gills well developed • tail over one-half final length, small, membranous fin • widely scattered melanophores over dorsum	• forelimbs develop beneath operculum • eye pigment well developed, slight choroid fissure • no external gills develop • fins low, poorly developed, slightly vascular (*Arenophryne*), or well developed and more vascular (*Myobatrachus*) • some fine melanophore stippling over brain and vertebral region
7	• hind limbs with obvious knee joints, foot paddles first evident • elbow visible on forelimbs • tail $^{2}/_{3}$ final length, fin almost full size, vascular	• foot develops up to 3 early toe nubs • one forelimb begins to break through operculum (*Arenophryne*) • tail at full length, fins remain low (*Arenophryne*) • beginning of first gut wall within yolk
9	• limbs elongate, digits on hands and feet • tail $^{2}/_{3}$ full length with full size fin • pigmentation expands to about midway down yolk	• forelimbs fully erupted in *Arenophryne*; still beneath operculum alongside head in *Myobatrachus*; toe digits similar to Gosner stages 35-36 • tail full length in both • pigmentation expands around sides and partly over venter • beginning of small, conical projection on inside centre of lower lip, small notch in centre of upper lip
10	• toes to $^{1}/_{3}$ of hatching length • pigmentation dense on dorsum, less on head	• forelimbs now erupted in *Myobatrachus*; toes all individually separate and a bit longer, similar to Gosner stage 37 • pigmentation uniform over entire dorsum and sides, denser over head and vertebral region
11-12	• tail full length with full fin • egg tooth first develops on upper lip by late stage 12	• tail at full length from stage 9 • nonkeratinised conical projection on inside lower lip
13	• toes full length, toe pads first evident • egg tooth develops keratin • yolk reserve still large	• limbs well advanced, subarticular tubercles develop on hands and feet, no toe pads • no egg tooth, nonkeratinised conical projection fits into deeper notch in upper lip when mouth closes • intestinal development now obscured by pigment
15	• tail remnant half or less of full length at hatching	• no tail remnant prior to hatching

yellow, mature ovarian eggs with a mean diameter of 4 mm. An adult male found on 1 April 1981 was sitting on a clutch of seven eggs buried in sand at a depth of 80 cm and soil temperature in the nest site at 0845 hr was 25°C. It was not possible to determine if there was a burrow leading to the frog and eggs, or a chamber around them, as the sand caved in during excavation. The eggs in stage 1 had a mean capsule diameter of 5.5 mm (5.0–6.0 mm) and initially adhered together in a cluster by means of the sticky outer surface of each capsule. As they became covered in sand, individual capsules separated. Another clutch at the same depth was unattended by an adult (Roberts 1984).

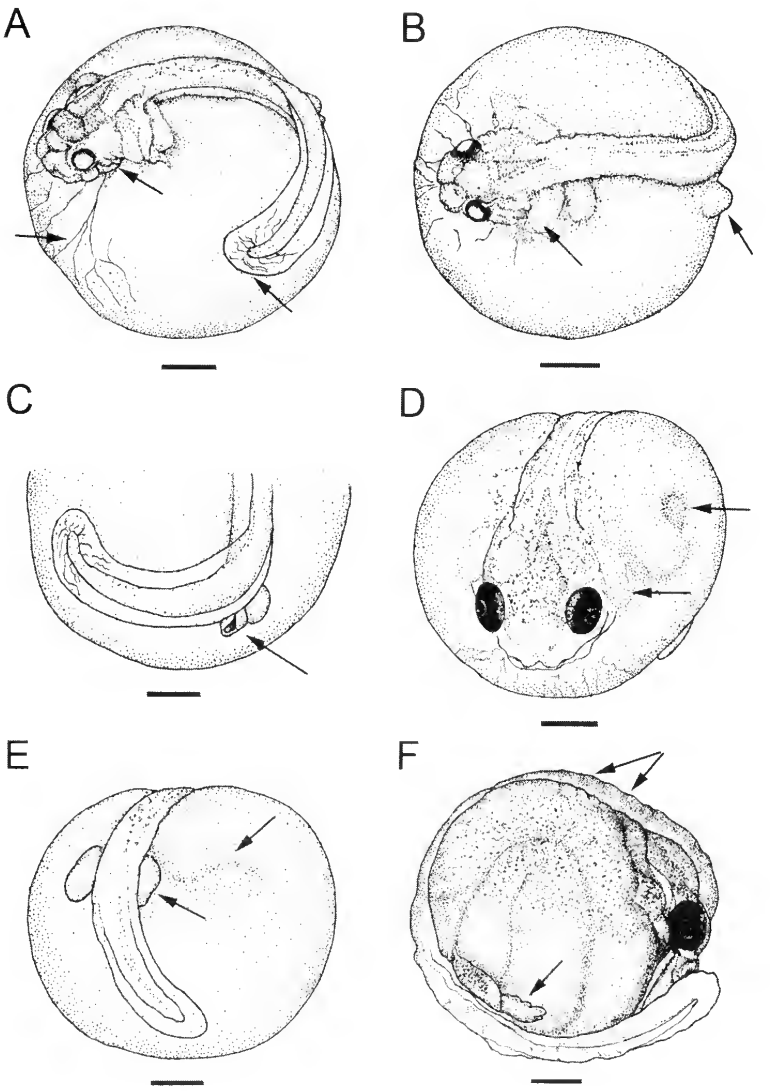


Figure 3 Stages 5, 6, and 9 (Townsend and Stewart, 1985) of *Myobatrachus gouldii*. A = stage 5, dorsal view; B and C = stage 5, dorsal and partial posterior views (line indicates forelimb beneath operculum in B and vent in C); D and E = stage 6, anterior and posterior views; and F = stage 9, lateral view. Scale bar represents 1 mm. Arrows indicate features highlighted in bold in Table 2.

Embryos at stages 1, 2–4, 6, 7, 9 and 15 are described in Table 1, and illustrated in Figures 1 and 2. Embryos are unpigmented during stages 1–4. Live embryos were not easily studied due to fine sand over the capsules. A pair of frogs collected on 1 April 1981, laid 11 eggs (clutch 4) some time between 1–3 April and cleavage furrows were observed during early to mid-cleavage on 4 April. Gastrulation and blastopore formation seemed typical of those described for aquatic tadpoles (Gosner 1960) and the dorsal lip was a distinct indentation. Estimating 2 April as the approximate date eggs were laid, late gastrula was reached after about 5 days and the neural plate began to form (stage 2) after about 10 days. Stage 5 was reached after about 16 days (none preserved) and stage 6 after 24 days.

Hatching and embryonic life span

Well formed froglets from clutch 4 were observed twitching within the capsules from about 45 days after the eggs were laid, and after about 50 days some were unhatched and adpressed tightly against the capsule wall with no yolk remaining. The last

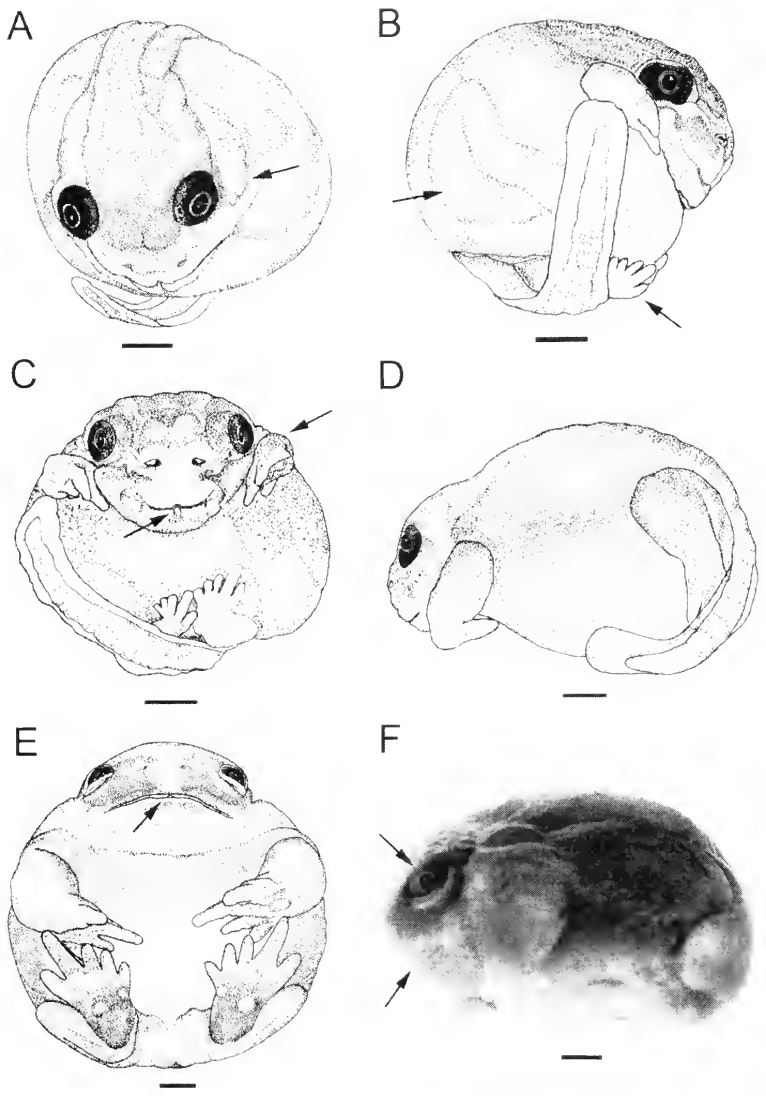


Figure 4 Stages 9, 10, 13 and 15 (Townsend and Stewart, 1985) of *Myobatrachus gouldii*. A = stage 9, anterior view, forelimb beneath operculum; B and C = stage 10, lateral and ventral views; D = stage 13, lateral view; and E and F = stage 15, ventral view and photograph of lateral view, just prior to hatching. Scale bar represents 1 mm. Arrows indicate features highlighted in bold in Table 2.

froglet hatched (yolk present in intestinal loops) on 12 June 1981, about 64 days after the eggs were laid (SV = 10.4 mm, weight 0.22 g). On 5 June, one froglet from another clutch which had been collected at stage 1 (dorsal lip to mid-gastrula) on 1 April, was found beginning to hatch with one hind limb extended through the capsule wall. When removed and washed to remove sand, the remaining jelly layers came free and the froglet became active and soon began to burrow (SV = 9.9 mm, weight 0.24 g). There was a distinct middorsal stripe and the remnant yolk mass was quite large. Minimum embryonic life span for this individual was about 65 days (estimating four days from fertilisation to mid-gastrula). Three recent hatchlings 1–2 weeks old measured 11.2–11.4 mm (mean 11.3 mm) and all weighed 0.25 g.

Development of *Myobatrachus gouldii*

Clutch sizes of fertilised and ovarian eggs ranged from 9–38 (mean 25, n = 5; Roberts 1981). The mean diameter of 28 ovarian eggs from a female caught in February 1979 is 5.1 mm, and mean diameters of 26, 38 and 9 ovarian eggs from three females collected

in November and December 1979 are 5.0, 5.3 and 4.9 mm, respectively (Roberts 1981). The mean capsule diameter of 23 live embryos from one clutch at early cell division collected in February 1979 is 7.4 mm (± 0.5 SD). The live embryos are creamy white, and the surface of the capsules are sticky to the touch, fairly tough and covered with fine sand. They soon become like firm, round balls to touch. Early cell division in live embryos at stage 1 is similar to that described for *Heleioporus eyrei* at Gosner stage 4 (Packer 1966) with four, dorsal micromeres and two perpendicular, incomplete cleavage furrows at the vegetal pole. Embryos at the earliest preserved stages available at stage 5 (T&S) have small limb buds, but unlike *E. coqui* at this stage, the eyes are partially pigmented (see Discussion).

Stages 5, 6, 9, 10, 11, 13 and 15 are described in Table 2, and illustrated in Figures 3 and 4.

Hatchlings

Hatching was not observed. Five fully formed froglets just prior to and just after hatching measured 8.9–10.8 mm (mean 10.1), were exact miniatures of the adult in form and pigmentation and began to burrow soon after hatching.

In summary, *A. rotunda* and *M. gouldii* share the following characteristics: large, unpigmented ova encapsulated with a thin outer layer (that becomes fairly tough) and an inner jelly layer, no external gills or adhesive organs, early limb bud development prior to any optic pigmentation, no spiracle and forelimbs covered by the operculum until at least stage 7. Eyes develop pigment gradually from stage 5 and increase noticeably in diameter during stages 6–8. The neural tube is initially raised above the large yolk (stages 4–5), gradually flattens and broadens from about stage 6 onward, then as vertebrae develop, the vertebral column appears as a broad, thickened ridge. The vent tube begins to develop from about stage 4, the gut gradually develops from initial divisions in the yolk at stage 6, into a thick intestinal coil by stage 9, and a small internal flap develops inside each naris from about stage 9.

The mouth begins as a small stomodaeal pit at stage 4, then becomes a simple slit that gradually widens with jaw development and never develops the oral mouthparts of a tadpole. During stage 9, a small flexible conical structure (visible when the mouth is opened) begins to project upwards from the inside centre of the lower lip and inserts into a corresponding notch centred in the upper lip; this projection becomes more defined in subsequent stages and the inner margin of the notch deepens posteriorly. These structures remain in the adult and are also present in the Australian microhylids (Anstis *unpublished observations*). Frog-like features of the head develop from as early as stage 9.

DISCUSSION

Comparative development

Although not all stages were available for the two species, an adequate comparative understanding of their development can be gained from the existing material, because in those stages where direct comparison was possible, similarities were quite evident and differences were minor. No pairs of adults for either species were observed in amplexus and the mode of fertilisation could not be determined, but as eggs are laid in sand, internal fertilisation could be advantageous. The relatively large size of the ova and the small clutch sizes are also characteristic of direct developing species (e.g., 2.0–10.0 mm and clutch sizes of 1–94; Thibaudeau and Altig 1999). Based on the similarity in early cell division noted here between *H. eyrei* and *M. gouldii*, it is likely that cleavage is holoblastic, but more live material needs to be studied to verify this. The tough external capsules may protect developing embryos but do not prevent desiccation in *M. gouldii* (Roberts 1981). Death by desiccation may be a result for embryos of both species if normal winter rains are delayed.

Arenophryne rotunda has a shorter tail with low fins and a narrower muscle and much narrower tail tip than *M. gouldii*. *Myobatrachus gouldii* has a long tail with more prominent fins that provide a greater degree of vascularisation, a broad muscle, broadly rounded tip and the tail is well advanced by stage 5 (Figure 3A, Table 3). Pigmentation is generally less dense in *A. rotunda* during stages 4–9. The forelimbs emerge through the epidermis during stage 7 for *A. rotunda* and about stage 10 for *M. gouldii*.

Arenophryne rotunda and *M. gouldii* have forward burrowing behaviour (Tyler *et al.* 1980; Main *et al.* 1959; Lindgren and Main 1961), and the minute flap in the narial canal which persists in adults, possibly prevents sand particles being lodged in the nostrils during burrowing.

Hatching

Hatching in these species has not been fully observed, but in *A. rotunda*, one embryo pushed a hind limb through the capsule wall at the onset of hatching. In a description of the hatching process of the microhylid *Cophixalus darlingtoni* from Papua New Guinea, Tyler (1976b) observed that prior to hatching, the embryo used only abrupt, outstretched movements of the arms and legs to split the capsule. From the one observation of the *A. rotunda* hatchling, it appears that the hatching process in *A. rotunda*, and probably *M. gouldii*, is similarly precipitated by abrupt movements of the limbs, since the outer layer of the jelly capsule is dry and tough and the embryos already have quite robust forelimbs.

The turgidity of the egg jellies of direct developers would seem to require the use of an egg tooth during hatching, and embryos of species of *Eleutherodactylus* are known to poke at the inside of the egg capsule with the keratinised egg tooth on the upper lip (Townsend and Stewart, 1985; Duellman and Trueb, 1986). In *A. rotunda* and *M. gouldii,* however, there is no egg tooth, only the small, nonkeratinised conical projection described.

Comparisons with Eleutherodactylus coqui

The two Australian myobatrachids differ from *E. coqui* in that they deposit eggs in subterranean sites, they do not develop an egg tooth, the initial development of the forelimbs is internal prior to stage 7 or 10 (exposed from stage 4 in *E. coqui*), the tail is more advanced in development by stage 5 (*M. gouldii*) and there are no external gills. Apart from the differences noted above and those in Table 3, they have a generally similar developmental life history to *E. coqui,* but it has not been possible to adequately compare aspects of gut, mouth and eye development (choroid fissure), vitelline circulation and behaviour.

Comparisons with other Australian myobatrachids and microhylids

Arenophryne rotunda and *Myobatrachus gouldii* share key features typical of direct development as defined by Altig and Johnston (1989) including the lack of mouthparts and a spiracle. The absence of a spiracle and mouthparts are also typical of other Australian endotrophic guilds including *Assa darlingtoni* and *Bryobatrachus nimbus* (Anstis 2002). The paraviviparous genus *Rheobatrachus* and the nidicolous species of *Geocrinia,* however, have a vestigial spiracle and much reduced mouthparts, including a few very small lateral marginal papillae and nonkeratinized jaw ridges (Anstis *unpublished observations*; Watson and Martin 1973; Tyler and Davies 1983). Adhesive glands are absent in *A. rotunda* and *M. gouldii* and in *Spicospina flammocaerulea* from southwestern Australia, a species with aquatic development in which the hatchlings are fully supported within thick algae mats (Dziminski and Anstis 2004), negating the need for adhesive glands.

Exposed forelimb bud development throughout embryonic stages is found in the microhylid genus *Cophixalus* (Tyler 1976b; Anstis *unpublished observations*) and also in the earlier stages of *Philoria,* which has terrestrial, nidicolous larvae. In at least three species of *Philoria* (*P. sphagnicolus, P. kundagungan* and *P. loveridgei*), all four limb buds are initially exposed from about Gosner stage 20, but the forelimbs are soon covered by the operculum and continue development internally during larval stages, breaking through the operculum at Gosner stage 42 (Anstis 1981; De Bavay 1993; Ingram and Corben 1975; Anstis 2002).

Further studies on the Australian direct developing genera are required to improve our understanding of their morphology, physiology and general biology, including mode of fertilisation, embryonic behaviour, life span and the hatching process, so that adequate future comparisons can be made with other direct developing genera.

ACKNOWLEDGEMENTS

The Western Australian Museum is gratefully acknowledged for the loan of the specimens studied. Field work and research was supported by the University of Western Australia. We thank the staff at the University of Western Australia for their assistance. K. Thumm and several reviewers offered helpful suggestions on the manuscript.

REFERENCES

Altig, R. and Johnston, G.F. (1989). Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs* **3**: 81–109.

Anstis, M. (1981). Breeding biology and range extension for the New South Wales frog *Kyarranus sphagnicolus* (Anura: Leptodactylidae). *Australian Journal of Herpetology* **1**: 1–9.

Anstis, M. (2002). *Tadpoles of south-eastern Australia: a guide with keys*. Reed New Holland, Sydney, Australia.

De Bavay, J. M. (1993). The developmental stages of the sphagnum frog, *Kyarranus sphagnicolus* Moore (Anura: Myobatrachidae). *Australian Journal of Zoology* **41**: 275–93.

Duellman, W.E. and Trueb, L. (1986). *Biology of Amphibians*. McGraw-Hill Book Company, New York.

Dziminski, M. A. and Anstis, M. (2004). Embryonic and larval development of the sunset frog, *Spicospina flammocaerulea* (Anura: Myobatrachidae), from southwestern Australia. *Copeia* **2004**: 893–899.

Frost, D.R., Grant, T., Faivovich, J., Bain, R., Haas, A., Haddad, C.F.B., de Sá, R.O., Donnellan, S.C., Raxworthy, C.J., Wilkinson, M., Channing, A., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D. and Wheeler, W.C. (2006). The amphibian tree of life. *Bulletin of American Museum of Natural History*. **297**: 1–370.

Gitlin, D. 1944. The development of *Eleutherodactylus portoricensis*. *Copeia* 1944: 91–98.

Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**: 183–190.

Ingram, G. J. and Corben, C.J. 1975. A new species of *Kyarranus* (Anura: Leptodactylidae) from Queensland, Australia. *Memoirs of the Queensland Museum*. **17**: 335–339.

Jameson, D. L. 1950. The development of *Eleutherodactylus latrans*. *Copeia* 1950: 44–46.

Lindgren, E., and Main, A.R. (1961). Natural history notes from Jigalong, IV: Frogs. *West Australian Naturalist* **7**: 193–195.

Main, A. R., Littlejohn, M.J. and Lee, A.K. (1959). Ecology of Australian frogs, p. 396–411. In *Biogeography and Ecology in Australia*, eds A. Keast, R. L. Crocker and C. S. Christian. Junk: The Hague.

Maxson, L. R. and Roberts, J.D. (1985). An immunological analysis of the phylogenetic relationships between two enigmatic frogs, *M. gouldii* and *A. rotunda*. *Journal of Zoology (London)* **207**: 289–300.

Packer, W. C. (1966). Embryonic and larval development of *Heleioporus eyrei* (Amphibia: Leptodactylidae). *Copeia* **1966**: 92–97.

Read, K., Keogh, J.S., Scott, I.A.W., Roberts, J.D. and Doughty, P. (2001). Molecular phylogeny of the Australian frog genera *Crinia* and *Geocrinia* and allied taxa (Anura: Myobatrachidae). *Molecular Phylogenetics and Evolution* **21**: 294–308.

Roberts, J. D. (1981). Terrestrial breeding in the Australian leptodactylid frog *Myobatrachus gouldii* (Gray). *Australian Wildlife Research* 8: 451–62.

Roberts, J. D. (1984). Terrestrial egg deposition and direct development in *Arenophryne rotunda* Tyler, a myobatrachid frog from coastal sand dunes at Shark Bay, W.A. *Australian Wildlife Research* **11**: 191–200.

Thibaudeau, G., and Altig, R. (1999). Endotrophic Anurans, p. 170–188. In *Tadpoles: the Biology of Anuran Larvae*, eds R. W. McDiarmid and R. Altig. University of Chicago Press, Chicago.

Townsend, D. S. and Stewart, M.M. (1985). Direct development in *Eleutherodactylus coqui* (Anura: Leptodactylidae): a staging table. *Copeia* **1985**: 423–436.

Tyler, M. J. (1962). On the preservation of anuran tadpoles. Australian Journal of Science **25**: 222.

Tyler, M. J. (1976a). A new genus and two new species of leptodactylid frogs from Western Australia. *Records of the Western Australian Museum* **4**: 45–52.

Tyler, M. J. (1976b). *Frogs*. Australian Naturalist Library. Collins, Australia.

Tyler, M. J., Roberts, J.D. and Davies, M. (1980). Field observations on *Arenophryne rotunda* Tyler, a leptodactylid frog of coastal sandhills. Australian Wildlife Research **7**: 295–304.

Tyler, M. J., Smith, L.A. and Johnstone, R.E. (2000). *Frogs of Western Australia*. Western Australian Museum, Perth.

Wake, M. H. 1978. The reproductive biology of *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae), with comments on the evolution of live-bearing systems. *Journal of Herpetology* **12**(2): 121–133.

Watson, G. F., and Martin, A. A. (1973). Life history, larval morphology and relationships of Australian leptodactylid frogs. *Transactions of the Royal Society of South Australia* **97**: 33–45.

APPENDIX 1

Collection and preservation dates (day/month/1981), stage (Townsend and Stewart 1985), and embryo dimensions (mm, diameters to stage 9, snout-vent length for stage 15) of *Arenophryne rotunda*. WAM = West Australian Museum. N = 1 in each case, see footnote.

Clutch	WAM	Coll.	Pres.	Stage	Dimensions
1	R97056	1/4	1/4	1	5.0
2	R97054	1/4	1/4	1	4.5x4.4
4	R97046	3/4	10/4	2	5.0
4	R97047	3/4	16/4	3	5.0x4.7
1	R97057	1/4	10/4	4	5.2x5.0
4	R97048	3/4	24/4	6[1]	5.0x4.2
3	R97049	1/4	16/4	6	5.1x4.5
3	R97050	1/4	24/4	7	4.8x4.6
4	R97052	1/4	15/5	7	5.7x4.7
1	R97059	1/4	24/4	9	5.6x5.5
3	R97053	1/4	22/5	15	6.6 SVL
1	R97060	1/4	1/5	15	4.8 SVL

[1] external egg diameter of one individual = 6.1 mm.

APPENDIX 2

Collection and preservation dates, stage (Townsend and Stewart 1985), and embryo dimensions (mm, diameters to stage 10, snout-vent length for stages 13–15) of *Myobatrachus gouldii*. WAM = West Australian Museum. N = 1 in each case, except R97037 = 4, range in parenthesis.

Clutch	WAM	Coll.	Pres.	Stage	Dimensions
1	R97036	4/3/81	4/3/81	5	5.7x5.6
1	R97036	4/3/81	4/3/81	5	5.7x5.7
1	R97037	4/3/81	13/3/81	6	5.1x5.5 (4.8–5.4x5.2–5.8)
1	R97038	4/3/81	27/3/81	9	6.4x6.2
1	R97040	4/3/81	16/4/81	9	6.6x6.4
1	R97039	4/3/81	3/4/81	10	6.1x5.8
2	R97041	14/4/82	14/4/82	13	8.5 SVL
3	R97042	14/4/82	14/4/82	15	10.8 SVL[1]
3	R97043	23/4/82	23/4/82	15	10.5 SVL
5	R97044	7/4/81	7/4/81	15	8.9 SVL
5	R97044	7/4/81	7/4/81	15	10.0 SVL[2]
4	R97945	14/4/81	14/4/81	15	10.1 SVL

[1] Egg dimensions = 11.3 x 10.8 mm

[2] Egg dimensions = 11.3 x 10.5 mm

Records of the Western Australian Museum **23**: 273–305 (2007).

Two new species of the *Delma tincta* group (Squamata: Pygopodidae) from northwestern Australia

Brad Maryan[1*], Ken P. Aplin[2], and Mark Adams[3]

[1] Department of Terrestrial Vertebrates, Western Australian Museum, Locked Bag 49 Welshpool DC, Perth, WA, 6986, Australia

[2] Australian National Wildlife Collection, CSIRO Division of Sustainable Ecosystems, PO Box 284 Canberra, ACT, 2601, Australia

[3] Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, SA, 5000, Australia

* Corresponding author

Abstract – Analysis of allozyme and morphological variation has revealed that two pygopodid lizard species are presently confused under *Delma pax* Kluge, 1974. *Delma pax* is redescribed and shown to be confined to the Pilbara region, while a closely related, new species is described from the arid deserts of western and central Australia. A second new species, endemic to the Cape Range Peninsula, is also described. Among Western Australian specimens previously referred to *D. borea* Kluge, 1974, those from the Pilbara islands are confirmed; however, all specimens from the Pilbara mainland and arid desert localities are reallocated to other taxa. Both of the newly described species belong to an expanded *Delma tincta* group which displays a complex biogeographic pattern in northwestern Australia. An updated key to the *Delma* spp. of Western Australia is provided.

INTRODUCTION

There are currently 25 described species of pygopodid lizard known from Western Australia (Wilson and Swan 2003). Of these, *Delma* is the most speciose genus with ten species, five of which were described in a comprehensive taxonomic revision by Kluge (1974a). Since this revision, several additional species and subspecies have been recognized in Western Australia, including *D. butleri* Storr, 1987, *D. haroldi* Storr, 1987 and *D. fraseri petersoni* Shea, 1991. Shea (1991) advocated synonymy of *D. haroldi* and *D. butleri* and this view is supported in a recent phylogenetic study of pygopodid lizards by Jennings *et al.* (2003). These authors also elevated *D. f. petersoni* to full species status and advocated transfer of *Aclys concinna* Kluge, 1974 to *Delma* [as suggested also by Kluge (1976)]. Aplin and Smith (2001) highlighted further taxonomic complexity in the widespread *D. australis* Kluge, 1974 and in *D. butleri*, with preliminary investigations suggesting that both are composites.

Shea (1991) proposed a *Delma tincta* group to include *D. tincta, D. borea* and *D. pax*, based on their similar patterning, the usual presence of a single large temporal scale bordering each parietal scale, and their largely allopatric pattern of geographic distributions. The integrity of this grouping was strongly supported by Jennings *et al.* (2003) analysis of DNA sequence variation among pygopodid lizards and by their combined morphological and molecular analysis. However, neither dataset was able to resolve the relationships among the three species.

Problems with the taxonomy of the *Delma tincta* group were noted by field herpetologists working in the Pilbara region in Western Australia. Application of a published key (Storr *et al.* 1990) resulted in some Pilbara specimens being identified as *D. borea* Kluge, 1974, which is otherwise known from the Kimberley region, Northern Territory, western Queensland (Kluge 1974; Shea 1987; Shea 1991) and northwestern South Australia (Ehmann 2005). Similar identification problems were apparent on the Cape Range Peninsula, where specimens initially identified as *D. pax* from the Exmouth region (Storr and Hanlon 1980) were subsequently transferred to *D. tincta* De Vis, 1888 (Storr *et al.* 1990).

This study presents molecular and morphological evidence for the recognition of two new species of *Delma* in northwestern Australia, both of which were previously confused with *D. pax* and/or *D. tincta*. The results further reinforce the opinion of Shea (1987) and others (e.g. Aplin and Smith 2001) that our knowledge of the taxonomy of the morphologically conservative genus *Delma* is far from complete.

METHODS

Morphological analysis

This study is based on the examination of material held in the Western Australian Museum (WAM), Northern Territory Museum (NTM), Australian Museum (AM) and South Australian Museum (SAM). The "R" prefix has been omitted for all WAM, NTM, AM and SAM specimens and, unless otherwise indicated, specimen registration numbers refer to the herpetological collection of the Western Australian Museum. Sex of individuals was determined by dissection and inspection of gonads; some immature or poorly preserved individuals were left unsexed. Head scale terminology, methods of scale counting and morphometric measurements follow those used by Shea (1987), except that all scales between postnasal and circumocular granules are counted as loreals (after Storr *et al.* 1990). Bilateral loreal counts were averaged if different.

For the purpose of this study the following morphometrics data were taken with digital vernier calipers and plastic ruler: snout-vent length (SVL), tail length (Tail L), head depth immediately behind eye (Head D), head length from tip of snout to posterior margin of ear (Head L), head width between ear (Head W), hindlimb length from junction of limb flap with body to distal tip of flap (Hindlimb L), mouth length from tip of snout to oral rictus (Mouth L), rostral depth between dorsal and ventral extremes of scale (Rostral D), rostral width between lateral extremes of scale (Rostral W), snout length from tip of snout to anterior margin of eye (Snout L) and eye width between anterior and posterior extremes of transparent cornea (Eye W). All measurements are reported in millimeters (mm) and characters recorded from the right side only. Specimens preserved in a circular or twisted position were straightened on a flat surface when measured for snout-vent and tail length. Tails were not measured if they were recently broken or obviously regenerated, as suggested by a clear break in colouration or patterning. However, x-rays are necessary to reliably distinguishable original and fully regenerated tails and these were not taken during this study. Accordingly, tail measurements are not used in any taxonomic sense and statistical data are provided for descriptive purposes only.

For each species, the possibility of sexual dimorphism in body measurements and scale counts were explored by Analysis of Variance (ANOVA), following tests for normality and homogeneity of variance. Pairwise interspecific statistical comparisons were similarly conducted, using pooled-sex or single sex samples as appropriate. Contrasts are regarded as statistically significant if p values were less than 0.05.

Because significant sexual dimorphism was observed in SVL for most species, variation in the size and proportions of the head was further examined by Analysis of Covariance (ANCOVA). For each taxon, Head L was first regressed against SVL for each sex and ANCOVA used to test for equality of the slopes and intercepts. All other dimensions were then regressed against Head L to test for differences in head proportions between the sexes.

Interspecific differences were explored by first preparing bivariate plots of all dimensions against SVL, separately for each sex. The head dimensions were then combined using Principal Component Analyses (PCA; based on covariance matrices) to produce a simplified representation of the morphometric variation. All analyses were performed on untransformed data after bivariate plots showed essentially linear patterns of relative growth among the various measures and no significant growth-related increase in variance in any dimension. Statistical analyses were performed with MINITAB Release 14.20 or GenStat Release 6.1.

All WAM specimens of *D. borea* and *D. tincta* collected subsequent to Kluge (1974) were assessed for three characters; supranasal scale division, midbody scale row count and the identity of the supralabial scale positioned beneath the eye to quantify the intraspecific variation and determine the effectiveness of these characters for identification. Due to their geographic proximity to the new species described herein, all specimens from the Western Australian Pilbara islands plus all available *D. borea* from the southern sector of the Northern Territory were also examined (see Appendix 1).

Allozyme analysis

Frozen liver or heart tissues for allozyme electrophoresis were obtained from the frozen tissue collections of the Western Australian and South Australian Museums for 12 specimens of typical *D. pax*, six specimens of the 'desert' morphotype, four specimens of the 'Cape Range' morphotype, and three specimens of each of *D. tincta* and *D. borea* from localities in northwestern Australia. We also included samples identified as *D. butleri* (n = 9) and *D. haroldi* (n = 4), drawn from across the geographic range of this sibling pair (or geographically variable taxon; Shea 1991). A total of 41 specimens were represented in the study (see Appendix 2 for voucher details). We used allozyme electrophoresis to test the hypothesis that each of the identified morphotypes within the *Delma tincta* group represents a distinct evolutionary species. The samples of *D. butleri* and *D. haroldi* were included as members of a second species group to provide a perspective on genetic diversity within the *D. tincta* group.

Allozyme electrophoresis was carried out on cellulose acetate gels (Cellogel©) using the principles and procedures detailed in Richardson *et al.* (1986). The following enzymes or non-enzymatic proteins displayed sufficient activity and resolution to allow allozymic interpretation:– aconitase hydratase (ACON, EC 4.2.1.3), acid phosphatase (ACP, EC 3.1.3.2), aminoacylase (ACYC, EC 3.5.1.14), adenosine deaminase (ADA, EC 3.5.4.4), alcohol dehydrogenase (ADH, EC 1.1.1.1), carbonate dehydratase (CA, EC 4.2.1.1), diaphorase (DIA, EC 1.6.99), enolase (ENOL, EC 4.2.1.11), esterase (EST, EC 3.1.1), fructose-bisphosphatase (FDP, EC 3.1.3.11), fumarate hydratase (FUM, EC 4.2.1.2), glyceraldehyde-3-phospate dehydrogenase (GAPD, EC 1.2.1.12), guanine deaminase (GDA, EC 3.5.4.3), lactoylglutathione lyase (GLO, EC 4.4.1.5), aspartate aminotransferase (GOT, EC 2.6.1.1), glycerol-3-phosphate dehydrogenase (GPD, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), guanylate kinase (GUK, EC 2.7.4.8), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), malate dehydrogenase (MDH, EC 1.1.1.37), "malic" enzyme (ME, EC 1.1.1.40), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), dipeptidase (PEPA, EC 3.4.13), tripeptide aminopeptidase (PEP-B, EC 3.4.11), proline dipeptidase (PEPD, EC 3.4.13), phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), phosphoglucomutase (PGM, EC 5.4.2.2), pyruvate kinase (PK, EC 2.7.1.40), superoxide dismutase (SOD, EC 1.15.1.1), L-iditol dehydrogenase (SRDH, EC 1.1.1.14) and triose-phosphate isomerase (TPI, EC 5.3.1.1). The nomenclature used to refer to loci and allozymes follows Adams *et al.* (1987).

The allozyme data were analysed in several ways. In the first instance, Principal Co-ordinates Analysis (PCoA) was employed to assess the genetic affinities of individuals, independently of any *a priori* grouping based on morphology. Following an initial PCoA on all 41 specimens analysed, subsequent PCoAs were then undertaken on each of the three subsets of specimens which clustered together and comprised more than one morphotypic form. The rationale underlying this 'stepwise' use of multiple PCoAs to identify genetic groups from first principles, plus the methodological details involved, are presented in Smith and Adams (2006).

Having defined the major genetic groupings using PCoA, the phylogenetic relationships among these groups were explored by constructing a Neighbor Joining tree from pairwise Nei's genetic distances. This analysis was undertaken using the NEIGHBOR computer program contained with PHYLIP 3.5c (Felsenstein 1993), and the resultant tree drawn using TREEVIEW (Page 1996). A measure of the robustness of clades was obtained by bootstrapping the allele frequency data for 100 pseudoreplicates, using a BASIC program written by M. Adams.

A second measure of genetic divergence was obtained by calculating the percentage fixed differences (% FDs) among groups. As argued by Richardson *et al.* (1986), the number of "fixed" or diagnostic differences between populations is more biologically relevant when determining species boundaries than are Nei D values, which may be quite large even in the absence of any genuinely diagnostic loci.

RESULTS

Morphological analysis

Initial recognition of the potential new species emerged during a careful examination of all *D. pax* specimens and of *D. borea* specimens from the southern Kimberley in Western Australia and from southern Northern Territory. During this morphological survey, special attention was paid to the identity of the supralabial scale positioned beneath the eye and the detail and intensity of head patterning at various stages of maturity. Using these characters in combination, it was possible to detect subtle but consistent differences between three morphologically diagnosable geographic entities. These were: (i) true *D. pax* from the Pilbara with strong juvenile head pattern that fades early in ontogeny, (ii) a distinctive, inornate 'Cape Range' morphotype with similarities to each of *D. pax* and *D. borea* and (iii) a widespread 'desert' morphotype with a persistent well-developed head pattern. Each of these taxa appeared to be quite distinct from each of *D. borea* and *D. tincta*.

Before undertaking any morphometric comparisons, we examined the linear measurements and scale counts from each of the putative taxa and geographically proximate samples of *D. borea* and *D. tincta* for evidence of sexual dimorphism. Statistically significant sexual dimorphism was observed in each species but with contrasting expression in each (Tables 1 and 2).

In all putative taxa, females are significantly longer bodied (SVL) than males. In typical *D. pax* and the 'desert' morphotype the mean SVL of females is 109% and 112% larger than that of conspecific males (Table 1). This value is slightly lower in *D. borea* (107%). The small sample of the 'Cape Range' morphotype gives an estimate of dimorphism of 112%. These observations are consistent with Kluge's (1974: 34) observation for pygopodids that "the female of a given species almost always attains a larger size than the male."

In each of *D. pax*, the 'desert' morphotype and *D.*

Table 1 Summary of mensural and meristic data gathered in this study, presented separately for each sex. The 'desert' and 'Cape Range' morphotypes are listed in this and all subsequent tables as *D. desmosa* and *D. tealei*, respectively, reflecting the ultimate taxonomic arrangement. Also shown are data for the redefined *D. pax* and for geographically proximate samples of *D. borea* and *D. tincta*. Values are mean ± one standard deviation, range and sample size (n).

		D. tealei	*D. desmosa*	*D. pax*	*D. borea*	*D. tincta*
SVL	♂	73.7 ± 1.49 70–77 (4)	70.0 ± 1.47 60–80 (24)	74.1 ± 1.42 55–93 (42)	70.0 ± 1.10 54–88 (42)	66.6 ± 1.72 58–72 (9)
	♀	82.2 ± 2.56 77–88 (4)	78.4 ± 2.53 56–90 (15)	81.0 ± 1.46 58–98 (39)	74.8 ± 1.18 54–95 (50)	79.4 ± 4.62 66–92 (5)
Tail L	♂	146.3 ± 33.0 107–212 (3)	198.2 ± 10.7 85–275 (24)	184.4 ± 7.67 109–271 (32)	172.9 ± 6.86 57–240 (35)	189.3 ± 17.61 102–263 (9)
	♀	142.2 ± 29.7 87–210 (4)	187.5 ± 13.0 80–257 (14)	198.5 ± 6.31 117–257 (33)	176.5 ± 9.21 53–259 (42)	228.6 ± 11.87 200–260 (5)
Ventrals	♂	50.5 ± 0.5 50–52 (4)	51.8 ± 0.30 48–56 (24)	54.2 ± 0.30 50–58 (43)	53.7 ± 0.46 47–62 (42)	48.7 ± 0.78 44–52 (9)
	♀	51.5 ± 0.5 50–52 (4)	52.9 ± 0.45 50–58 (15)	56.0 ± 0.32 52–60 (39)	54.3 ± 0.34 50–58 (50)	52.4 ± 0.68 50–58 (5)
Head L	♂	8.50 ± 0.09 8.36–8.77 (4)	8.04 ± 0.13 7.08–9.28 (24)	8.51 ± 0.10 6.96–9.88 (43)	8.13 ± 0.09 6.79–9.39 (42)	7.58 ± 0.16 6.96–8.22 (9)
	♀	8.81 ± 0.27 8.18–9.39 (4)	8.52 ± 0.16 7.21–9.65 (15)	8.72 ± 0.10 7.45–9.78 (39)	8.34 ± 0.10 6.68–9.89 (50)	8.20 ± 0.35 7.16–9.02 (5)
Head W	♂	5.55 ± 0.09 5.35–5.75 (4)	4.76 ± 0.08 3.91–5.54 (24)	5.11 ± 0.08 3.96–6.48 (43)	4.82 ± 0.08 3.91–5.99 (42)	4.52 ± 0.16 3.88–5.24 (9)
	♀	5.53 ± 0.23 5.11–6.16 (4)	5.11 ± 0.15 3.85–6.06 (15)	5.34 ± 0.10 3.71–6.73 (39)	5.01 ± 0.07 3.69–6.06 (50)	4.77 ± 0.32 3.97–5.59 (5)
Head D	♂	4.49 ± 0.27 3.85–5.04 (4)	4.39 ± 0.08 3.60–5.13 (24)	4.52 ± 0.07 3.51–5.97 (43)	3.91 ± 0.07 3.16–5.04 (42)	3.79 ± 0.10 3.35–4.39 (9)
	♀	4.44 ± 0.13 4.11–4.73 (4)	4.70 ± 0.15 3.61–5.65 (14)	4.68 ± 0.12 3.33–6.25 (39)	4.07 ± 0.07 3.06–5.45 (49)	3.94 ± 0.22 3.44–4.52 (4)
Mouth L	♂	5.89 ± 0.14 5.51–6.18 (4)	5.83 ± 0.12 4.88–6.84 (24)	6.29 ± 0.12 5.24–8.40 (43)	5.65 ± 0.08 4.63–6.79 (42)	6.23 ± 0.21 4.87–6.99 (9)
	♀	5.85 ± 0.11 5.59–6.13 (4)	6.19 ± 0.14 4.99–6.93 (15)	6.49 ± 0.10 5.02–7.99 (39)	5.80 ± 0.07 4.51–6.82 (50)	6.71 ± 0.34 5.76–7.89 (5)

tincta the number of enlarged ventral scales is significantly higher in females than males (Table 2), with mean ventral scale counts in females being 1.8, 1.1 and 3.7 (scales) greater than the conspecific male values, respectively (Table 1). In contrast, *D. borea* and the 'Cape Range' morphotype do not show significant sexual dimorphism in this feature, although in each case the mean value for females is

Table 1 (cont.)

		D. tealei	*D. desmosa*	*D. pax*	*D. borea*	*D. tincta*
Snout L	♂	3.53 ± 0.11 3.32–3.78 (4)	3.19 ± 0.06 2.33–3.86 (24)	3.46 ± 0.05 2.74–4.76 (43)	3.28 ± 0.04 2.69–4.07 (42)	3.06 ± 0.10 2.76–3.76 (9)
	♀	3.51 ± 0.11 3.35–3.84 (4)	3.39 ± 0.09 2.61–3.93 (15)	3.52 ± 0.05 2.96–4.29 (39)	3.40 ± 0.04 2.63–4.09 (50)	3.39 ± 0.21 2.76–4.00 (5)
Rostral W	♂	1.88 ± 0.05 1.77–2.01 (4)	1.62 ± 0.04 0.93–1.88 (24)	1.66 ± 0.02 1.26–2.06 (43)	1.54 ± 0.02 1.23–1.84 (42)	1.44 ± 0.03 1.28–1.66 (9)
	♀	1.85 ± 0.08 1.63–2.06 (4)	1.79 ± 0.04 1.51–2.27 (15)	1.78 ± 0.03 1.40–2.19 (38)	1.58 ± 0.02 1.17–1.98 (50)	1.61 ± 0.06 1.48–1.87 (5)
Rostral D	♂	0.92 ± 0.07 0.76–1.10 (4)	0.95 ± 0.02 0.52–1.24 (24)	1.03 ± 0.02 0.81–1.25 (43)	0.87 ± 0.01 0.71–1.16 (42)	1.00 ± 0.03 0.81–1.14 (9)
	♀	1.09 ± 0.06 0.93–1.25 (4)	1.00 ± 0.03 0.67–1.18 (15)	1.06 ± 0.01 0.84–1.33 (38)	0.89 ± 0.01 0.64–1.21 (50)	0.98 ± 0.06 0.73–1.06 (5)
Eye W	♂	1.73 ± 0.13 1.48–2.04 (4)	1.46 ± 0.04 0.83–1.74 (24)	1.56 ± 0.02 1.23–1.84 (42)	1.50 ± 0.02 1.34–1.79 (42)	1.55 ± 0.07 1.16–1.88 (9)
	♀	1.97 ± 0.14 1.56–2.13 (4)	1.54 ± 0.04 1.16–1.79 (15)	1.56 ± 0.02 1.28–1.93 (39)	1.49 ± 0.02 1.19–1.81 (50)	1.60 ± 0.08 1.39–1.79 (5)
Hindlimb L	♂	3.20 ± 0.21 2.91–3.81 (4)	3.63 ± 0.10 2.59–4.42 (24)	3.60 ± 0.09 1.70–4.92 (43)	2.61 ± 0.05 1.73–3.43 (41)	2.63 ± 0.14 1.73–3.16 (9)
	♀	2.89 ± 0.27 2.08–3.31 (4)	2.89 ± 0.13 1.95–3.53 (15)	2.62 ± 0.06 1.95–3.80 (39)	2.10 ± 0.04 1.46–2.95 (49)	2.38 ± 0.16 1.99–2.95 (5)
Loreals	♂	7.25 ± 0.66 6–9 (4)	6.85 ± 0.22 5–9 (24)	7.37 ± 0.18 5–10 (43)	7.50 ± 0.19 4–9 (40)	4.96 ± 0.20 4–6 (9)
	♀	6.25 ± 0.48 5–7 (4)	6.87 ± 0.29 5–8 (15)	7.54 ± 0.19 5–10 (39)	7.24 ± 0.19 4–11 (50)	5.30 ± 0.46 4.5–7 (5)
Hindlimb scales	♂	8 ± 0.00 8 (4)	8 ± 0.00 8 (24)	8.51 ± 0.88 8–10 (43)	8.00 ± 1.25 5–10 (41)	5 ± 0.00 5 (9)
	♀	8 ± 0.00 8 (4)	8 ± 0.00 8 (15)	8.56 ± 0.91 8–10 (39)	7.66 ± 1.17 5–9 (50)	5 ± 0.00 5 (5)

higher than that for males. Kluge (1974) reported significant sexual dimorphism in mean ventral counts (always greater in females than males) in four species of *Delma* [*D. australis*, *D. impar* (Fischer, 1882), *D. nasuta* Kluge, 1974, and *D. tincta*], with means differing by 3–5 scales in each case. Species that Kluge (1974) found to be non-dimorphic in this attribute include *D. borea*, *D. fraseri* Gray, 1831, *D. grayii* Smith, 1849, *D. inornata* Kluge, 1974, *D. molleri* Lütken, 1863 and *D. plebeia* De Vis, 1888. Kluge's (1974) samples of *D. nasuta* and *D. inornata* were both composites as they both included specimens subsequently referred to *D. butleri* (Storr 1987; Shea 1991).

Sexual dimorphism in hindlimb length is expressed in each of *D. pax*, the 'desert'

Table 2 Statistical analysis (ANOVA) of intraspecific sexual dimorphism in selected mensural and meristic characters for each of *D. tealei*, *D. desmosa*, *D. pax*, *D. borea*, and *D. tincta*.

	D. tealei	*D. desmosa*	*D. pax*	*D. borea*	*D. tincta*
SVL	F = 8.218 d.f. = 1,7 P = 0.029	F = 9.600 d.f. = 1,38 P = 0.004	F = 11.380 d.f. = 1,80 P = 0.001	F = 8.311 d.f. = 1,91 P = 0.005	F = 9.753 d.f. = 1,13 P = 0.009
Tail L	F = 0.008 d.f. = 1,6 P = 0.931	F = 0.387 d.f. = 1,37 P = 0.538	F = 2.027 d.f. = 1,64 P = 0.160	F = 0.093 d.f. = 1,76 P = 0.761	F = 2.364 d.f. = 1,13 P = 0.150
Ventrals	F = 2.000 d.f. = 1,7 P = 0.207	F = 5.231 d.f. = 1,38 P = 0.028	F = 17.595 d.f. = 1,81 P <0.001	F = 1.175 d.f. = 1,91 P = 0.281	F = 10.105 d.f. = 1,13 P = 0.008
Head L	F = 1.108 d.f. = 1,7 P = 0.330	F = 4.933 d.f. = 1,38 P = 0.033	F = 1.995 d.f. = 1,81 P = 0.162	F = 2.274 d.f. = 1,91 P = 0.135	F = 3.407 d.f. = 1,13 P = 0.090
Head W	F = 0.008 d.f. = 1,7 P = 0.931	F = 4.464 d.f. = 1,38 P = 0.041	F = 2.967 d.f. = 1,81 P = 0.089	F = 2.839 d.f. = 1,91 P = 0.096	F = 0.576 d.f. = 1,13 P = 0.463
Head D	F = 0.0296 d.f. = 1,7 P = 0.869	F = 3.741 d.f. = 1,37 P = 0.061	F = 1.246 d.f. = 1,81 P = 0.268	F = 2.591 d.f. = 1,90 P = 0.111	F = 0.498 d.f. = 1,12 P = 0.495
Mouth L	F = 0.047 d.f. = 1,7 P = 0.835	F = 3.296 d.f. = 1,38 P = 0.078	F = 1.508 d.f. = 1,81 P = 0.223	F = 1.706 d.f. = 1,91 P = 0.195	F = 1.543 d.f. = 1,13 P = 0.238
Snout L	F = 0.016 d.f. = 1,7 P = 0.904	F = 3.044 d.f. = 1,38 P = 0.089	F = 0.536 d.f. = 1,81 P = 0.466	F = 2.955 d.f. = 1,91 P = 0.089	F = 2.513 d.f. = 1,13 P = 0.139
Rostral W	F = 0.084 d.f. = 1,7 P = 0.781	F = 5.659 d.f. = 1,38 P = 0.023	F = 7.498 d.f. = 1,80 P = 0.008	F = 1.582 d.f. = 1,91 P = 0.212	F = 6.231 d.f. = 1,13 P = 0.028
Rostral D	F = 2.894 d.f. = 1,7 P = 0.140	F = 1.354 d.f. = 1,38 P = 0.252	F = 1.320 d.f. = 1,80 P = 0.254	F = 0.837 d.f. = 1,91 P = 0.363	F = 0.101 d.f. = 1,13 P = 0.756
Eye W	F = 1.555 d.f. = 1,7 P = 0.259	F = 1.622 d.f. = 1,38 P = 0.211	F = 0.001 d.f. = 1,80 P = 0.979	F = 0.149 d.f. = 1,91 P = 0.700	F = 0.208 d.f. = 1,13 P = 0.657
Hindlimb L	F = 0.839 d.f. = 1,7 P = 0.395	F = 18.702 d.f. = 1,38 P <0.001	F = 65.496 d.f. = 1,81 P <0.001	F = 49.009 d.f. = 1,89 P <0.001	F = 1.103 d.f. = 1,13 P = 0.314
Loreals	F = 1.500 d.f. = 1,7 P = 0.267	F = 0.001 d.f. = 1,38 P = 0.973	F = 0.405 d.f. = 1,81 P = 0.526	F = 0.887 d.f. = 1,89 P = 0.349	F = 0.641 d.f. = 1,13 P = 0.439

morphotype and *D. borea*, with males having longer hindlimb flaps in each taxon (Table 1). Bivariate plots of this measurement against SVL for each of these taxa (Figure 1A–C) show that variance in hindlimb length is low at early growth stages (low SVL) and that sexual dimorphism emerges through life as a result of more rapid growth of the hindlimb, relative to SVL, in males than females. The different relative growth trajectory of each sex is confirmed by results of ANCOVA for each of *D. pax* and *D. borea* (Table 3). Results for the 'desert' morphotype are not statistically significant but this may be due to the lack of smaller females in the sample. Too few individuals of the 'Cape Range' morphotype were available and too few specimens of *D. tincta* were examined to determine the extent of hindlimb sexual dimorphism in each of these taxa. Somewhat surprisingly, the number of hindlimb scales is not sexually dimorphic in any of the studied species (Table 1). Kluge (1974) did not

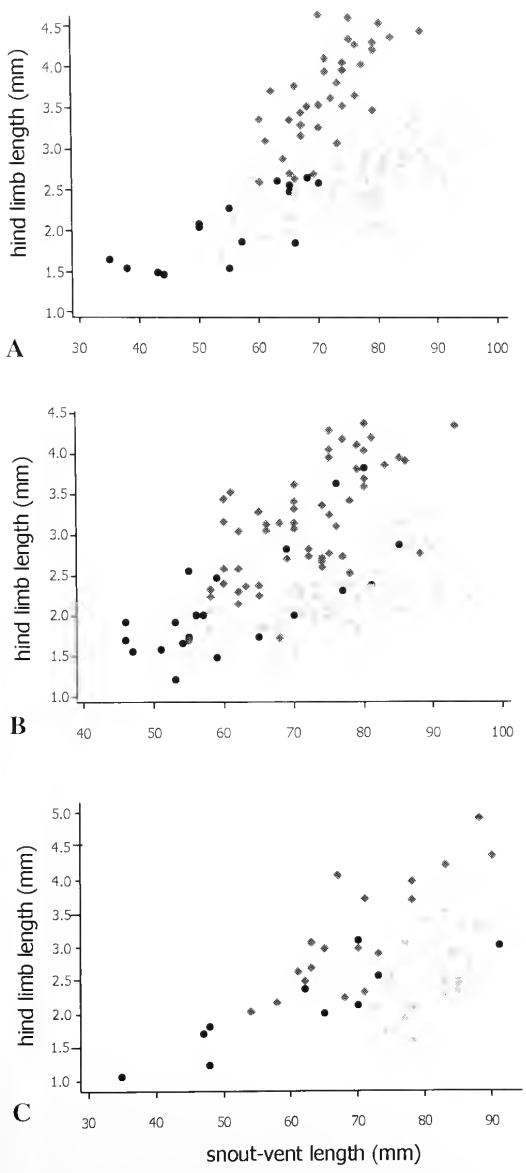


Figure 1 Bivariate plots of Hindlimb L against SVL for each of *D. pax* (A); *D. borea* (B) and the 'desert' morphotype (C). In each plot, males (diamonds) are distinguished from females (squares) and unsexed individuals (circles). The plots demonstrate that male-biased sexual dimorphism in hindlimb length in each species arises through more rapid growth of this appendage in males than in females.

present hindlimb lengths but did report a lack of sexual dimorphism in hindlimb scale counts in all *Delma* species.

For head dimensions, only a few statistically significant or near significant contrasts (Table 2) are observed between the sexes in each of *D. pax* (Head W, Rostral W), *D. borea* (Head W, Snout L), with mean values for females exceeding those of males in all cases. In contrast, the 'desert' morphotype shows female-biased sexual dimorphism in most head dimensions. Examination of bivariate plots of each head dimension against SVL (Figure 2A–C) indicate a clear lack of sexual dimorphism in *D. borea*, with no differences in the slopes or intercepts of regression lines, but a more complex situation in each of *D. pax* and the 'desert' morphotype. In these taxa, regression slopes are slightly higher in males than females, indicating a more rapid growth of the head relative to SVL in males than in females. However, for both taxa ANCOVA-s were not significant for any head dimension against SVL (Table 3). Bivariate plots of all other head dimensions against Head L for each taxon failed to reveal any sexual dimorphism in head proportions (Figure 2D–F for Head W against Head L) and this was also confirmed by non-significant results from ANCOVA (not shown). Males in each of these species of *Delma* thus develop a slightly larger head than females through life, but without any obvious proportional changes.

No sexual dimorphism was observed in loreal counts. This finding is consistent with that of Kluge (1974) for other *Delma* species and for pygopodids generally. Uniquely among pygopodids, *Lialis burtonis* Gray, 1835 is sexually dimorphic in the number of supralabial scales (Kluge 1974: 132).

Table 4 gives a summary of pairwise statistical comparisons among *D. pax*, *D. desmosa* and *D. borea* for various measurements and scale counts, with separate comparisons for each sex. Comments on statistically significant contrasts are provided under the individual species accounts.

For head dimensions, interspecific contrasts were examined separately for each sex by bivariate plots and then by PCA (results not shown). No clear interspecific differences were found. Instead, the head appears to be remarkably conservative in proportions among all of the species examined.

Allozyme analysis

We were able to score a total of 43 presumptive allozyme loci. Nine loci (*Est1, Gapd, Idh1, Lap, Ldh1, Ldh2, Mdh, Pk,* and *Tpi*) were invariant and hence uninformative for assessing genetic relationships among individuals. Appendix 2 presents the allozyme profiles of the 41 specimens examined at the 34 variable loci.

The initial PCoA on all specimens revealed the presence of four discrete clusters, labeled A–D on

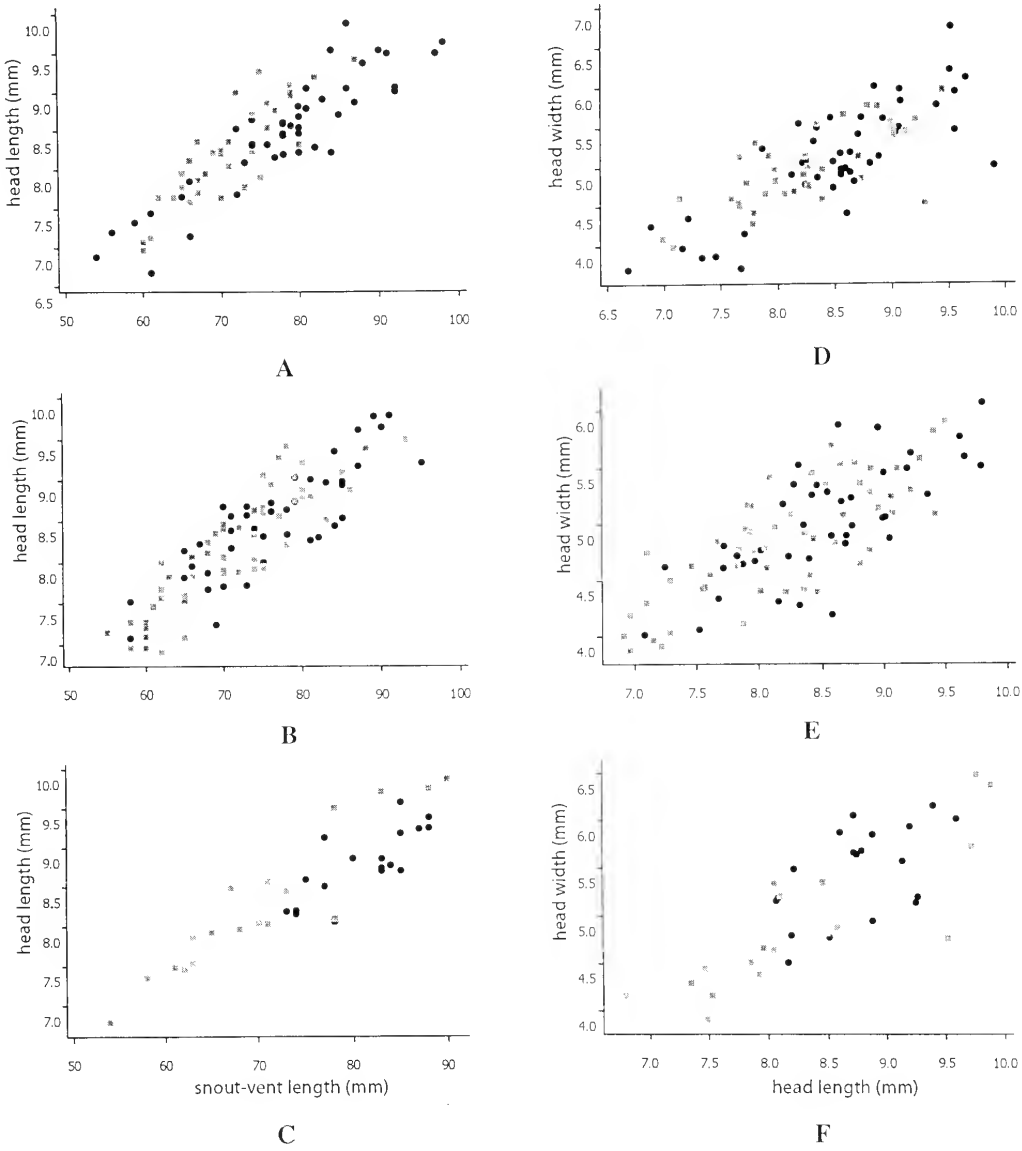


Figure 2 Bivariate plots of Head L against SVL and Head W against Head L for each of *D. pax* (A, D); *D. borea* (B, E) and the 'desert' morphotype (C, F). In each plot, males (squares) are distinguished from females (circles). The plots demonstrate slightly more rapid growth of the head relative to SVL in each of *D. pax* and the 'desert' morphotype, and a lack of differentiation between the sexes in head proportions.

Figure 3. As shown, only group D comprised specimens of a single *a priori* taxon (i.e. *D. tincta*). All other groups were composites: group A comprised specimens displaying either the *pax* or 'desert' morphotype, group B contained specimens referable to the 'Cape Range' morphotype or *D. borea*, and group C was a mix of both *D. butleri* and *D. haroldi*.

In order to determine whether all taxa were independently diagnosable by their allozyme profiles, a second round of PCoAs was undertaken on individuals within each of the composite groups A, B, and C (Figure 4). Unequivocal discrimination was indeed obtained between *D. pax* and the 'desert' morphotype (Figure 4A) and between *D. borea* and the 'Cape Range' morphotype (Figure 4B). The outcome was more complex for group C, since while *haroldi* was distinguishable from

Table 3 Statistical analysis (ANCOVA) of intraspecific sexual dimorphism for hindlimb and selected head dimensions for each of *D. borea*, *D. desmosa* and *D. pax*. Regression values are slope (a) ± s.e. and intercept (i). All regressions are highly significant and all contrasts passed tests of homogeneity of variance.

Comparison	SEX	Hindlimb L vs SVL		Head L vs SVL		Head L vs Head W	Loreals
D. borea	♂	a = 0.052 ± 0.007 i = 0.590	F = 5.67 d.f. = 1,92	a = 0.073 ± 0.006 i = 2.99	F = 2.06 d.f. = 1,94	a = 0.565 ± 0.065 i = 0.230	F = 0.01 d.f. = 1,94
	♀	a = 0.025 ± 0.009 i = 0.30	P = 0.019	a = 0.061 ± 0.007 i = 3.88	P = 0.155	a = 0.554 ± 0.086 i = 0.310	P = 0.921
D. pax	♂	a = 0.065 ± 0.010 i = –1.15	F = 35.93 d.f. = 1,79	a = 0.082 ± 0.009 i = 2.41	F = 2.44 d.f. = 1,79	a = 0.547 ± 0.103 i = 0.443	F = 2.54 d.f. = 1,80
	♀	a = 0.027 ± 0.005 i = 0.27	P < 0.001	a = 0.066 ± 0.005 i = 3.33	P = 0.123	a = 0.752 ± 0.077 i = –1.297	P = 0.115
D. desmosa	♂	a = 0.072 ± 0.012 i = –1.83	F = 0.24 d.f. = 1,36	a = 0.085 ± 0.008 i = 2.33	F = 0.52 d.f. = 1,36	a = 0.676 ± 0.111 i = –0.699	F = 0.19 d.f. = 1,36
	♀	a = 0.059 ± 0.023 i = –2.20	P = 0.624	a = 0.073 ± 0.015 i = 2.87	P = 0.477	a = 0.572 ± 0.208 i = 0.450	P = 0.662

Table 4 Statistical analysis of pairwise interspecific differences between each of *D. desmosa*, *D. pax*, and *D. borea* for selected mensural and meristic characters. The available sample of *D. tealei* is too small to yield significant results.

Comparison	SEX	SVL	Ventrals	Head L	Eye W	Hindlimb L	Loreals
pax vs *desmosa*	♂	F = 3.582 d.f. = 1,65 P = 0.063	F = 27.707 d.f. = 1,66 P <0.001	F = 7.002 d.f. = 1,66 P = 0.010	F = 5.452 d.f. = 1,65 P = 0.023	F = 0.037 d.f. = 1,66 P = 0.847	F = 3.149 d.f. = 1,66 P = 0.081
	♀	F = 0.817 d.f. = 1,53 P = 0.370	F = 27.178 d.f. = 1,53 P <0.001	F = 1.113 d.f. = 1,53 P = 0.296	F = 0.318 d.f. = 1,53 P = 0.575	F = 3.936 d.f. = 1,53 P = 0.053	F = 3.560 d.f. = 1,53 P = 0.065
pax vs *borea*	♂	F = 5.118 d.f. = 1,83 P = 0.026	F = 0.612 d.f. = 1,84 P = 0.436	F = 7.084 d.f. = 1,84 P = 0.009	F = 4.618 d.f. = 1,83 P = 0.035	F = 73.475 d.f. = 1,83 P <0.001	F = 0.237 d.f. = 1,82 P = 0.628
	♀	F = 11.196 d.f. = 1,88 P = 0.001	F = 12.295 d.f. = 1,88 P = 0.001	F = 6.860 d.f. = 1,88 P = 0.010	F = 6.391 d.f. = 1,88 P = 0.013	F = 45.916 d.f. = 1,87 P <0.001	F = 1.173 d.f. = 1,88 P = 0.282
desmosa vs *borea*	♂	F = 1.232 d.f. = 1,107 P = 0.270	F = 16.981 d.f. = 1,108 P <0.001	F = 3.264 d.f. = 1,108 P = 0.074	F = 1.015 d.f. = 1,65 P = 0.318	F = 10.466 d.f. = 1,107 P = 0.002	F = 4.551 d.f. = 1,63 P = 0.037
	♀	F = 0.131 d.f. = 1,103 P = 0.718	F = 11.240 d.f. = 1,103 P = 0.001	F = 0.004 d.f. = 1,103 P = 0.952	F = 1.385 d.f. = 1,64 P = 0.244	F = 19.146 d.f. = 1,102 P <0.001	F = 0.931 d.f. = 1,64 P = 0.338

butleri, the latter also displayed considerable heterogeneity which broadly manifested itself as three geographically-based clusters herein referred to as 'western', 'central', and 'eastern' (Figure 4C, Appendix 1). Thus the final outcome of the four PCoAs was the recognition of nine Operational Taxonomic Units (OTUs) among the 41 specimens examined, each diagnosable from all others using stepwise PCoA of the allozyme data. Table 5 compares allele frequencies for each OTU at the 34 informative loci, while Table 6 presents pairwise genetic distance (Nei D and % fixed difference) values.

In general, each of the OTUs is well-differentiated genetically from all others, with only five of the 36 pairwise comparisons involving fewer than six fixed differences (equivalent to 12%FD). Regarding the five exceptions, all but one occurred among the four OTUs identified within group C (*butleri/haroldi*); indeed, in the case of *D. haroldi* versus 'central' *D. butleri* the two OTUs shared alleles at all loci (0 %FD, Table 6).

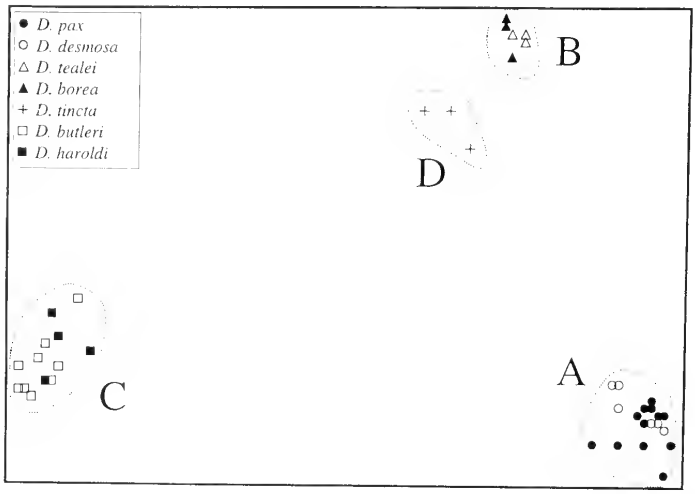


Figure 3 Principal Co-ordinates Analysis of the 41 specimens included in the allozyme study. The 'desert' and 'Cape Range' morphotypes are listed in this and all subsequent figures as *D. desmosa* and *D. tealei*, respectively, reflecting the ultimate taxonomic arrangement. The relative PCoA scores have been plotted for the first (X-axis) and second (Y-axis) dimensions, which individually explained 43% and 14% respectively of the total multivariate variation.

The only other pairwise comparison not characterized by multiple fixed differences is that between typical *pax* and the 'desert' morphotype. These OTUs displayed a single fixed difference (= 2%FD) and a modest Nei D of 0.08 (Table 6). In contrast, the 'Cape Range' morphotype shows fixed differences at 21% of loci to each of *D. pax* and the 'desert' morphotype (Nei D = 0.25–0.27) and a closer association with *D. borea* (12%FD and Nei D = 0.16). Pairwise contrasts within the *D. butleri/haroldi* group range from 0–14% for fixed differences and 0.04 to 0.21 for Nei D, with a closer affinity between *D. haroldi* and eastern *D. butleri* on the one hand, and between 'western' and 'central' populations of *D. butleri* on the other.

The Neighbour-Joining tree constructed from pairwise Nei D values (Figure 5) shows a deep division of the OTUs into two groups, one containing *D. butleri* and *D. haroldi*, and the other containing *D. tincta*, *D. pax* and *D. borea* and both the 'desert' and 'Cape Range' morphotypes. Within this latter group, *D. tincta* appears to be the most divergent, with the remaining four OTUs forming a common group made up of two pairs of OTUs: *pax* + 'desert' and *borea* + 'Cape Range'.

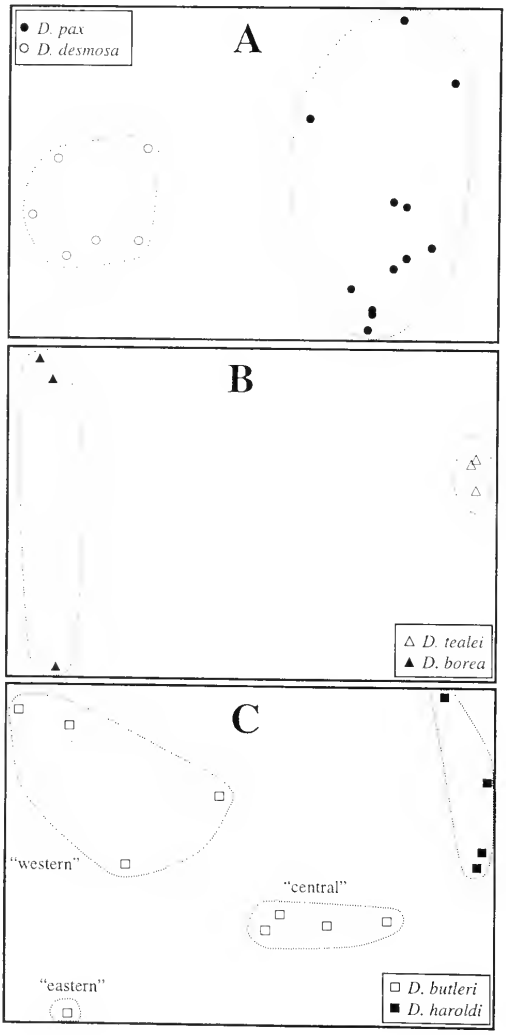


Figure 4 Principal Co-ordinates Analyses for each of the three groups identified in the initial PCoA (Figure 3). A) PCoA of group A specimens; the first and second dimensions individually explained 34% and 13% respectively of the total variance. B) PCoA of group B specimens; the first and second dimensions individually explained 75% and 16% respectively of the total variance. C) PCoA of group C specimens; the first and second dimensions individually explained 26% and 15% respectively of the total variance. Codes, legends, and general layout as per Figure 3.

Table 5 Allele frequencies at 34 variable loci for the nine OTUs identified in the allozyme study. For polymorphic loci, the frequencies of all but the rarer/rarest alleles are expressed as percentages and shown as superscripts (allowing the frequency of each rare allele to be calculated by subtraction from 100%). A dash indicates no genotypes assignable at this locus.

Locus	*pax*	*desmosa*	*tealei*	*borea*	*tincta*	*butleri* "western"	*butleri* "central"	*butleri* "eastern"	*haroldi*
Acon1	a	a	a	a	a	b^{88},c	a^{50},b	b	a^{75},b
Acon2	d^{96},b	c^{67},d	c	c^{83},d	b^{50},c^{33},a	a^{88},b	d	d^{50},e	a^{38},d^{37},c
Acp1	a	a	a	b	a	a	a	a	a
Acp2	b	b	b	b	a	a	a	a	a
Acyc	b^{62},a	b	a	a	a^{67},b	a	a	a	a^{75},c
Ada	b	b^{92},c	b	b	b^{67},d	b	b	b	b^{87},a
Adh1	b	c^{75},b	b	b	b	b	b^{87},a	b	b
Adh2	d	a^{50},c	c	c	a	c	b^{63},c	c	b
Ca	a	a	a	a	a	b	b	b	b
Dia	b^{71},e	b^{70},a	h^{88},j	h^{66},g^{17},d	g^{83},h	g^{75},i	c^{25},f^{25},g^{13},i^{13},h^{12},j	g	–
Enol	c	c	b	c	c	c^{62},b^{25},a	c	c	c^{75},b
Est2	d^{63},e	d	b	b^{67},c	b^{75},a	b	b	b	b^{88},c
Fdp	c	c^{92},b	a	a	a	a	a	a	a
Fum	b	b	b	b	b	b^{88},d	b^{88},d	b^{50},c	b^{75},a^{13},d
Gda	c	c	e	d	d	c^{87},a	c	c	c^{87},b
Glo	c^{96},b	c^{83},a	c	c	c	d	d	d	d
Got1	b^{96},a	b	b	b	b	b	b	c	b
Got2	b^{83},a	a	b	b	b	c	c	c	c^{75},d
Gpd	b	b	b	b	b^{67},a	b	b	b	b
Gpi	b	b^{92},a	b	b	b	c	c	c	c
Guk	b^{75},a	b	b	a^{83},b	a	a	a	a	a
Idh2	c	c	c	c	c	b^{87},a	b	b	b^{75},a^{13},d
Me1	c	c^{67},a	c	c	c	b^{75},c	b	b	c^{87},b
Mpi	b	b	b	b	b	a	a	a	a
Ndpk1	a	a	a	a	a	b	b	b	b
Ndpk2	b	b^{83},c	b	b^{83},a	b	b	b^{88},d	b	b
PepA	c^{62},b	c	c	c	c	c^{87},a	c	d	c
PepB	f^{96},e	f^{92},d	e	e	e	e^{75},b	e^{62},b	a	b^{50},e^{25},a^{13},c
PepD	c^{54},d	d^{58},c	c^{87},a	d^{50},c^{33},f	d^{83},b	d^{63},c^{25},f	d	c^{50},d	d^{63},f^{13},e^{12},g
6Pgd	b^{88},c	b	b^{87},a	b	b^{67},c	d	d	e	d
Pgm1	c	c^{70},b	e	g	d	c^{67},a	e^{88},f	f	e^{88},f
Pgm2	a	a	a	a^{83},b	a	a	a	a	a
Sod	d^{96},g	d	d	c	d	d	d^{75},a	d	a^{50},b^{25},e^{13},f
Srdh	b^{92},a	b	b	b	d^{67},b	b^{50},c	c	c	c

Table 6 Genetic distance matrices for the nine OTUs of *Delma* identified by the Principal Co-ordinates Analyses. Lower triangle = %FDs; upper triangle = Nei Ds

OTU	*pax*	*desmosa*	*tealei*	*borea*	*tincta*	*butleri* "western"	*butleri* "central"	*butleri* "eastern"	*haroldi*
pax	–	0.08	0.25	0.27	0.27	0.55	0.55	0.68	0.53
desmosa	2	–	0.27	0.30	0.31	0.58	0.61	0.74	0.59
tealei	21	21	–	0.16	0.27	0.48	0.53	0.68	0.49
borea	21	23	12	–	0.17	0.50	0.54	0.67	0.49
tincta	21	21	16	12	–	0.40	0.43	0.56	0.40
butleri 'western'	37	40	35	35	28	–	0.07	0.13	0.10
butleri 'central'	40	42	37	35	33	5	–	0.15	0.04
butleri 'eastern'	47	49	49	44	42	14	9	–	0.21
haroldi	38	43	36	36	31	7	0	12	–

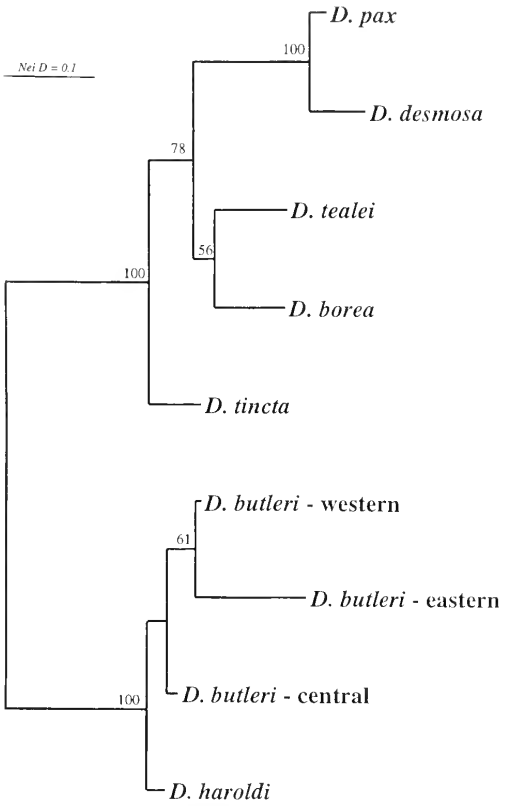


Figure 5 Neighbor-joining tree depicting the phylogenetic affinities of nine OTUs of *Delma*, based on Nei distances and rooted at the midpoint of the longest branch. Bootstrap proportions of 50% or greater from 100 pseudo-replications are indicated for all nodes. Scale represents a Nei D of 0.1.

The case for recognition of the 'Cape Range' morphotype as a distinct species is strongly supported by the genetic evidence. Although this population was historically associated first with *D. pax* and then with *D. tincta*, its genetic affinities clearly lie with *D. borea*. Nevertheless, the 'Cape Range' morphotype and *D. borea* are well-differentiated genetically, with a total of six fixed differences and a Nei D of 0.16 between them. This is equivalent to the observed genetic differentiation between *D. borea* and *D. tincta* (12%FD and Nei D of 0.17), two species that are broadly sympatric (but rarely syntopic; Shea 1991) across northern Australia. Furthermore, the 'Cape Range' morphotype is readily distinguished on several morphological criteria from *D. borea* (see below).

In contrast, the 'desert' morphotype is weakly differentiated from typical *D. pax*, with only a single observed fixed difference in their allozyme profiles. Despite this, there remains a strong case for treating these morphologically distinct populations as discrete evolutionary lineages. First, in addition to their single fixed difference at the *Adh2* locus, they also displayed major differences in allele frequency at a further three loci (*Acon2*[a] DP = 63%, *Adh1*[b] DP = 75%, *Got2*[b] DP = 83%; Table 5). Second, the spatial distribution of variation in each of the 'near fixed' loci within each taxon is not clustered in specific localities around the periphery of the Pilbara, as might be expected if regular gene flow was occurring between the two morphotypes, nor is it arranged in any geographic pattern that might be identified as a genetic cline. Last, each of the *D. pax* and the 'desert' morphotypes have quite large geographic distributions (see below), which nevertheless appear to abut around the perimeter of the Pilbara uplands, involving a total distance of many hundreds of kilometres. Such a geographic arrangement ought to facilitate gene flow between the two forms, yet they appear to maintain their morphological distinctiveness across their ranges.

In the following section we diagnose two new species of *Delma*, redefine *D. pax* as a taxon restricted to the Pilbara uplands, and comment on the distribution and morphology of *D. borea* populations in Western Australia.

SYSTEMATICS

Delma tealei sp. nov.
Figures 6–7

Material examined

Holotype

153811 in the Western Australian Museum, an adult female collected on 12 September 2003 by B. Maryan and D. Algaba on Charles Knife Road, Cape Range, Western Australia (22°07'08"S 114°03'44"E). Liver sample preserved in –75°C ultrafreeze at W.A. Museum.

Paratypes

Sex indicated in brackets.

Western Australia: 52934-35 (both F) Shothole Canyon (22°03'S 114°02'E); 82532 (M) 6 km W Exmouth (21°56'S 114°04'E); 88548 (F) 2 km E Yardie Creek mouth (22°20'S 113°49'E); 102837 (M) Cape Range National Park (22°09'01"S 113°59'52"E); 153813 (M) 2 km S Yardie Homestead Caravan Park (21°53'37"S 114°00'34"E); 153819 (M) Shothole Canyon (22°03'49"S 114°00'42"E).

Diagnosis

A moderately small species of *Delma* (SVL up to 88mm) with modally 14 midbody scales, two pairs of supranasals and relatively plain colouration apart from variegated ventrolateral scales on forebody.

Figure 6 Holotype (153811) of *Delma tealei*, photographed in life (B. Maryan).

Adults lack any trace of dark markings on head or neck. Differs from the otherwise similar *D. borea* in lower modal midbody scale count, typically the third supralabial positioned below the eye, absence of pattern on head and neck in adults and longer hindlimb flaps in both sexes.

Description

Rostral with obtuse apex, penetrating between rostral supranasals; two pairs of supranasals, caudal pair much larger; rostral supranasals in moderate contact with first supralabial; caudal supranasals in point to moderate contact with nostril; postnasal single; loreals 5–9, subequal; suboculars 3–4; supraciliaries 5, fifth much larger; supraoculars 2, second wider than first; supralabials 5, third elongate and positioned below eye, fifth much smaller; infralabials 4, third elongate; occipital scale present; upper temporals 2. General form of head and details of scalation illustrated in Figure 7. Midbody scale rows 14; transversely enlarged ventral scales 50–52; hindlimb scales 8.

Morphological Variation: 82532 has a small scale partly wedged between second and third supralabial on left side; 52934 has upper temporals divided on both sides.

Colouration and patterning

In preservative, upper and lateral surfaces light grey or light to dark brown, head slightly darker. Supralabials pale to dark brown and infralabials pale with brownish vertical streaks or blotches mostly centered on first and third sutures along series. Lateral scales on forebody typically variegated, bases greyish white to white, centres blackish (mostly a dark smudge) and apices greyish

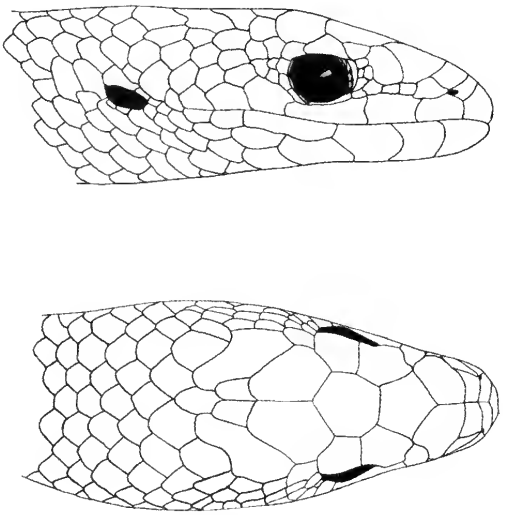


Figure 7 Head scalation of *Delma tealei* holotype (153811) in lateral (top) and dorsal (bottom) views.

to brownish grey. Variation includes individuals (e.g., 102837) with barely discernible variegation; and others (e.g., 52934) with distinct white-centred scales bordered by black smudging and with light brown apices. Lower surface greyish white or white with diffuse dark smudging on posterior edges of some scales.

In life, a subtle pinkish flush is noticeable on the dorsal and lateral scales immediately forward of and behind vent (e.g., 153811, 153813, 153819); this colour is lost in preservative.

No immature specimens are available for this

species. Accordingly, it is not known whether or not it displays the ontogenetic fading of head and neck patterning displayed by *D. pax* and some *D. borea* (see below for details).

Details of Holotype

Snout-vent length (mm) 79; tail 210; loreals 8; midbody scale rows 14; ventrals 52; hindlimb scales 8. Light grey upper and lateral surface, supralabials smudged grey aligned with dark vertical streaks on infralabial sutures 1–3, variegated lateral scales on forebody bases greyish white, apices greyish and some scales with blackish centres. Lower surface white and unpatterned.

Etymology

Named for zoologist Mr Roy Teale, in recognition of his contribution to Western Australian natural history and the collections of the Western Australian Museum, and his active support of numerous taxonomic research projects.

Distribution and sympatry

Apparently restricted to the Cape Range Peninsula of North West Cape in Western Australia (Figure 8), a heavily dissected limestone plateau, sparsely vegetated with *Triodia*, shrubs and low eucalypts; gorges within the range are more heavily vegetated (Storr and Hanlon 1980).

Three other species of *Delma* are recorded on the Cape Range Peninsula. *Delma nasuta* Kluge, 1974 and *D. tincta* De Vis, 1888 are known from multiple localities and the regional sample is consistent with other populations of these widespread taxon. A third taxon, currently associated with *D. australis* Kluge, 1974 of southern Australia, is known from a single specimen (132470) collected at Shothole Canyon. Specimens of *D. tincta* were collected on the same occasion as *D. tealei* at four localities (Shothole Canyon, 52933; Cape Range National Park, 102838; 2 km S Yardie Homestead Caravan Park, 153814; Charles Knife Road, 153820).

Comparison with other species

Delma tealei will be compared first with *D. borea* and *D. tincta*, the two species with which it is most similar to, then with each of the regionally sympatric *D. nasuta* and *D. australis*, and finally with geographically distant congeners with which it shares important characters.

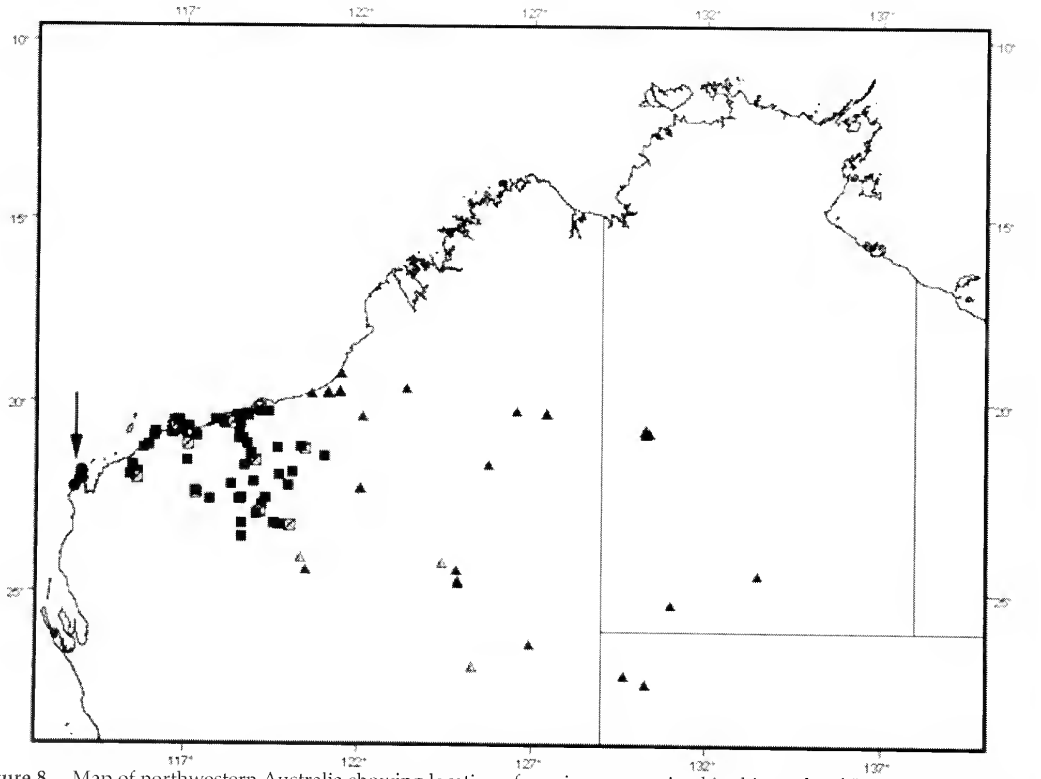


Figure 8 Map of northwestern Australia showing location of specimens examined in this study of *Delma tealei* (circles with arrow), *Delma desmosa* (triangles) and *Delma pax* (squares). Open symbols with cross indicate specimens examined in allozyme analysis.

Delma tealei is morphologically most similar to populations of *D. borea* on the western Pilbara islands (e.g., 28656, 37371, 37406, 48559). These taxa are similar in body size and share two pairs of supranasals and some indication of variegated ventrolateral scales on the forebody. However, all populations of *D. borea* have higher midbody scale row counts (modally 16 versus 14), some indication in adults of pale brown bands on the head and neck, and typically the fourth supralabial positioned below the eye (typically the third in *D. tealei*).

Delma tealei and *D. tincta* share modally 14 midbody scales and indication of variegated ventrolateral scales on the forebody. *Delma tincta* has one pair of supranasals (two pairs in *D. tealei*) and dark dorsal head markings that are especially distinctive on immature specimens but remain visible on most adult specimens (Storr *et al.* 1990) including individuals (e.g., 52933, 102838, 153814) from some of the same localities as the new species. *Delma tincta* also has smaller hindlimb flaps than *D. tealei* (Table 1). The hindlimb scale counts are correspondingly lower in *D. tincta* (5 versus 8).

Delma nasuta from Cape Range Peninsula and elsewhere grows to larger size (SVL up to 112mm versus 88mm) and has a more elongate snout, higher midbody scale row counts (modally 16 or 18 versus 14), more loreals (6–23 versus 5–9) and a reticulated or spotted body pattern formed by a dark spot or emargination on numerous body scales.

The Cape Range Peninsula specimen of *D. 'australis'* is smaller than *D. tealei* (SVL 57mm versus up to 88mm) and further differs in having one pair of supranasals (versus two), more midbody scale rows (modally 18 versus 14), and very different patterning that includes fine black lateral bars on the neck and throat. It also shares an unusual arrangement of the loreal scales with typical *D. australis* (loreal row is broken by prefrontal-supralabial contact versus continuous in *D. tealei*).

Delma pax and *D. desmosa* are both allopatric to *D. tealei* (Figure 8). They are distinguished by higher midbody scale row counts (modally 16 versus 14) and uniformly coloured ventrolateral scales on the forebody. Adult *D. desmosa* differ further by the ontogenetic retention of dark dorsal head markings.

Habitat

The holotype was raked (using a 3-prong cultivator) from dead *Triodia* clumps on a low hill vegetated with *Triodia* and sparse shrubs on brown stony loam (Figure 9). The paratypes were collected in the same manner except for 88548 that was found beneath an exfoliated limestone slab on heavy *Eucalyptus* leaf litter, and 102837 that was pit-trapped in a valley floor surrounded by low limestone breakaways (P. Kendrick, *pers. comm.*). All collection sites for this species combine hummock grass and limestone, an association that is overwhelmingly dominant on the Cape Range Peninsula.

Figure 9 Low stony hills covered with dense *Triodia* at the Charles Knife Road, Cape Range WA, the type locality for *Delma tealei* (B. Maryan).

Remarks

Delma tealei was originally thought to represent a southern outlier population of *D. pax* when first collected during herpetofaunal surveys (Storr and Hanlon 1980). The combination of two pairs of supranasals and third upper labial in subocular position probably influenced this decision. However, in preparation for publication of a handbook to the gekkonoid lizards of Western Australia (Storr *et al.* 1990), fresh examination resulted in the transfer of this population to *D. tincta*. This action probably reflected the shared condition of 14 midbody scale rows in each of *D. tealei* and *D. tincta*.

In Storr *et al.* (1990) the species account for *D. tincta* (incorporating *D. tealei*) included the statement 'usually one (occasionally two) pairs of supranasals' but without reference to a specific population. We consulted Kluge (1974) and also examined all Western Australian Museum holdings of *D. tincta* (see Appendix 1) to ascertain whether this statement holds true following exclusion of *D. tealei*. Kluge (1974) examined 168 specimens and encountered a single individual (22323) with unilateral division (left side) of the supranasals. Similarly, in a total of 163 specimens examined by us, we found only one example (104426) with bilateral division into two pairs of asymmetrically shaped supranasals, and another (85190) with unilateral division (right side). Both of these examinations suggest that any individual variation away from the conditional state of undivided supranasals in *D. tincta* is extremely rare. Accordingly, we believe that the reference by Storr *et al.* (1990) to supranasal multiplication in *D. tincta* was in specific reference to specimens from the Cape Range Peninsula referred herein to *D. tealei*. *Delma inornata* from eastern Australia appears to be the only species of *Delma* that exhibits regular intraspecific variation (around 10%) in having either 1 or 2 pairs of supranasals (Kluge 1974: 103). Among Western Australian *Delma* the combination of 14 midbody scale rows and 2 pairs of supranasals is unique to *D. tealei*.

Delma tealei would probably receive an IUCN conservation rating of 'Least Concern' on account of the lack of evidence for any population decline and most of its geographic range being protected within the Cape Range National Park. However, in many areas on the Cape Range Peninsula, introduced Buffel Grass (*Cenchrus ciliaris*), has virtually replaced the original ground cover (Aplin 1998) and there is an identified priority to monitor and manage its spread (Keighery and Gibson 1993). Particular attention should be given to the impact on species such as *Delma tealei* that are probably dependent on *Triodia* and other hummock grasses for their survival.

Delma desmosa sp. nov.

Figures 10–12

Material examined

Holotype

102657 in the Western Australian Museum, an adult female collected on 10 October 1996 by S. van Leeuwen at Site Cooma 4, Little Sandy Desert, Western Australia (24°06'17"S 120°19'30"E). Liver sample preserved in –75°C ultrafreeze at W.A. Museum.

Paratypes

Sex indicated in brackets.

Western Australia: NTM 17987 (M) Sandfire Flat (19°47'S 121°09'E); 45809-10 (both M) Wallal Downs Homestead (19°47'S 120°38'E); 63313 (M) Djaluwon Creek (20°20'S 127°26'E); 64001 (M) Anketell Ridge (20°24'S 122°07'E); 64097 (F) Statfords Bore (20°21'S 127°24'E); 64143 (F) Breaden Pool (20°15'S 126°34'E); 64186 (F) 1 km S Waddawalla Well (21°41'S 125°46'E); 75798 (F) Dragon Tree Soak (19°39'S 123°23'E); 75830 (M) Anna Plains Homestead (19°15'S 121°29'E); 87007 (F) Sandfire Roadhouse (19°46'S 121°06'E); 87353 (M) 3 km SE Wallal Downs Homestead (19°47'S 120°40"E); 88535-41 (M, F, F, F, M, F, F) 55 km S Anna Plains Homestead (19°44'S 121°28'E); 94757, 94776-77 (F, M) 80 km S Telfer Mine (22°20'12"S 122°02'26"E); AM 100853, 101548 (both M) 6.6 km N Sandfire Roadhouse (19°19'S 121°16'E); 102650 (M) Cooma 5, Little Sandy Desert (24°06'41"S 120°19'10"E); 108477 (M) 18 km S Lake Hancock (24°27'S 124°50'E); 114555 (F) Sandfire Roadhouse (19°46'S 121°06'E); 126496 (M), 126498 (M) Gibson Desert Nature Reserve (24°43'S 124°52'E); 132802 Warri Airstrip (24°15'S 124°24'E); 139089 (M) Mandora Station (19°45'16"S 121°26'59"E); 140442 (M) Yanneri Lake (24°27'08"S 120°29'02"E); 145073 (M) Officer Basin area (26°55'58"S 125°16'44"E); 151252 (F) Townsend Ridges (26°20'25"S 126°56'26"E). **Northern Territory:** NTM 14901 (F) 12 km SW Sangsters Bore (20°52'S 130°16'E); NTM 15038 (M) Uluru National Park (25°21'S 131°01'E); NTM R15138 (M), NTM 15144 (M), NTM 15146 (F), NTM 15151 (M) 12 km SW Sangsters Bore (20°52'S 130°16'E); NTM 15230 (M) 17 km W Sangsters Bore (20°48'S 130°14'E); NTM 15501 (M) Uluru National Park (25°21'S 131°01'E); NTM 20250 (M) Sangsters Bore (20°51'09"S 130°23'09"E); NTM 26789 Henbury (24°34'S 133°30'E); NTM 32301 (M) 10 km WSW Sangsters Bore (20°44'S 130°16'E); NTM 34489 (F) Ayers Rock (25°20'S 131°01'E). **South Australia:** SAM 48671 (M) 9.3 km NNW Cheeseman Peak (27°19'46"S 130°17'36"E); SAM 59561 (F) 3.3 km W Mount Holder, Birksgate Range (27°08'43"S 129°39'51"E).

Figure 10 Holotype (102657) of *Delma desmosa*, photographed in life (B. Maryan).

Diagnosis

A moderately small, stout species of *Delma* (SVL up to 90mm) with modally 16 midbody scales, two pairs of supranasals and distinctive dark dorsal head markings present throughout life (any ontogenetic fading is restricted to markings forward of the eyes).

Description

Rostral with obtuse apex, penetrating between rostral supranasals; two pairs of supranasals, caudal pair much larger; rostral supranasals in moderate contact with first supralabial and caudal supranasals in point contact or only narrowly separated from the nostril; postnasal single; loreals 3–9, subequal; suboculars 3–4; supraciliaries 5, fifth much larger; supraoculars 2, second wider than first; supralabials 5–6, third typically elongate and positioned below eye (rarely, fourth is below eye); posteriormost supralabial much smaller; infralabials 4 (rarely 5), third elongate; occipital present; upper temporals 2.

General form of head and details of scalation illustrated in Figure 11. Midbody scale rows 16; transversely enlarged ventral scales 48–59; hindlimb scales 8–10.

Morphological Variation: 75798 and 132802 have third supralabial divided on left side; 94757 has this scale divided on both sides. The location of accessory supralabial suture (e.g., anterior, centre or posterior) determines whether it is the third or fourth that is positioned below the eye.

64186 has third infralabial divided on right side; 114555 has this scale divided on both sides.

64097 has second supraocular fused with fourth supraciliary on both sides.

63313 has an upper loreal that is interposed between first and second loreals and contacts second supralabial on both sides.

88539 has supraoculars fused into one scale on right side.

NTM 15146 has a small scale interposed between caudal pair of supranasals and rostral supranasals divided into two scales on right side.

AM 100583 has first supraciliary fused with an upper loreal on right side.

AM 101548 has three small scales interposed between third and fourth supraciliary on right side.

Colouration and patterning

In preservative, upper and lateral surface grey to greyish brown merging with light brown on tail (particularly regenerated portion). Irregular black smudging on dorsal scales in some individuals (e.g., 64186, 88537, 15038, 15151, 15501). Lateral scales on forebody are plain. Lower surface immaculate white.

Head of juveniles and adults typically with three to four dark brown to black dorsal to lateral bands, that narrow as they descend and terminate obtusely

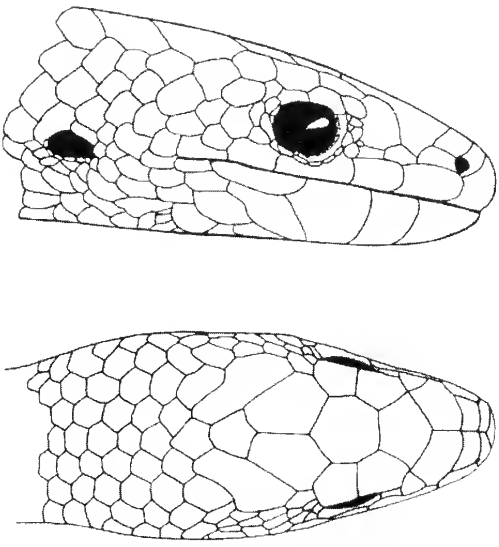


Figure 11 Head scalation of *Delma desmosa* holotype (102657) in lateral (top) and dorsal (bottom) views.

on mental scale, on infralabials and behind the ear. Dark head bands are most intense on immature specimens (Figure 12A) but remain well-defined in most adults (Figure 12C; ontogenetic fading is a common occurrence in other *Delma* spp.). Interspaces between dark bands light brown, greyish to white and usually widest on back of head through ear and neck. Supralabials and infralabials whitish in between dark bands. Below the mouth, bands are typically centred on suture between mental and first infralabial, and on suture between second and third infralabials; suture between first and second infralabials is invariably clear; occasionally, the first dark head band completely covers the first infralabial but not its anterior suture (e.g., 140442).

In adults that show signs of ontogenetic fading of the head pattern (Figure 12B), the first band (on snout and lores) and second band (over eyes) typically become diffuse and merge to form a cream to light brown colour forward of eyes. The broader third and fourth dark bands (forward of and behind ears, respectively) are persistent in adults and are rarely diffuse or broken. In some individuals (e.g., 15038, 34489, 88537) coalescent dark smudges positioned transversely across forebody are suggestive of a fifth dark band. Adult specimens of *D. desmosa* with pronounced ontogenetic fading come from localities spread across the western half of the range of the species, including localities in the Great Sandy Desert (e.g., 64097, 64143, 75830) that are remote from the range of *D. pax* in the Pilbara region. The wide geographic distribution of these individuals make it unlikely that they are the product of introgression between *D. pax* and *D. desmosa*.

In life, some adults have pale orange-brown interspaces between the dark bands; this pigment is lost in preservative.

Details of Holotype

Snout-vent length (mm) 87; tail 163; loreals 8 on left side, 9 on right; midbody scale rows 16; ventrals 59; hindlimb scales 9. Greyish brown upper and lateral surface.

Indication of four dark brown head bands as follows: first on lores is diffuse and terminates as smudge on first infralabial; second terminates on suture between second and third infralabial, leaving preceding suture clear white; third and fourth bands are dark brown and well-defined.

Etymology

From the Greek *desmos*, a chain, tie, or band, in specific reference to the distinctive and persistent dorsal head bands of this species.

Distribution and sympatry

Widespread in arid desert regions of western and central Australia (Figure 8) extending west to the vicinity of the 80 mile beach (Anna Plains and Wallal Downs Stations), south to the Little Sandy Desert and Officer Basin area and east through the Great Sandy, Tanami and Great Victoria Deserts into central Northern Territory (Sangsters Bore, Uluru National Park and Henbury) and northwestern South Australia (Cheeseman Peak).

The geographic distributions of *D. desmosa* and *D. pax* appear to be allopatric (Figure 8). Currently the two species are known to occur within 90 km of each other (e.g., 102650, 102657 from Little Sandy Desert versus 125452 from 30 km E Newman, respectively). Specimens from these proximate localities do not show any admixture of characters as might be expected if significant levels of gene flow were occurring across a contact zone or step cline.

Five *Delma* species have geographic distributions that overlap that of *D. desmosa*: *D. borea, D. butleri, D. haroldi, D. nasuta* and *D. tincta*. Among these species, the greatest morphological similarity occurs between *D. desmosa* and *D. borea* (see below). The distributions of *D. borea* and *D. desmosa* are broadly overlapping in the south Kimberley, southern Northern Territory and northwestern South Australia (Figures 8, 15) but there are few known instances of actual sympatry. Recent collections by P. Kendrick of the Department of Environment and Conservation have extended the mainland W.A. range of *D. borea* south to the vicinity of Mandora (e.g., 112725-26, 139058,

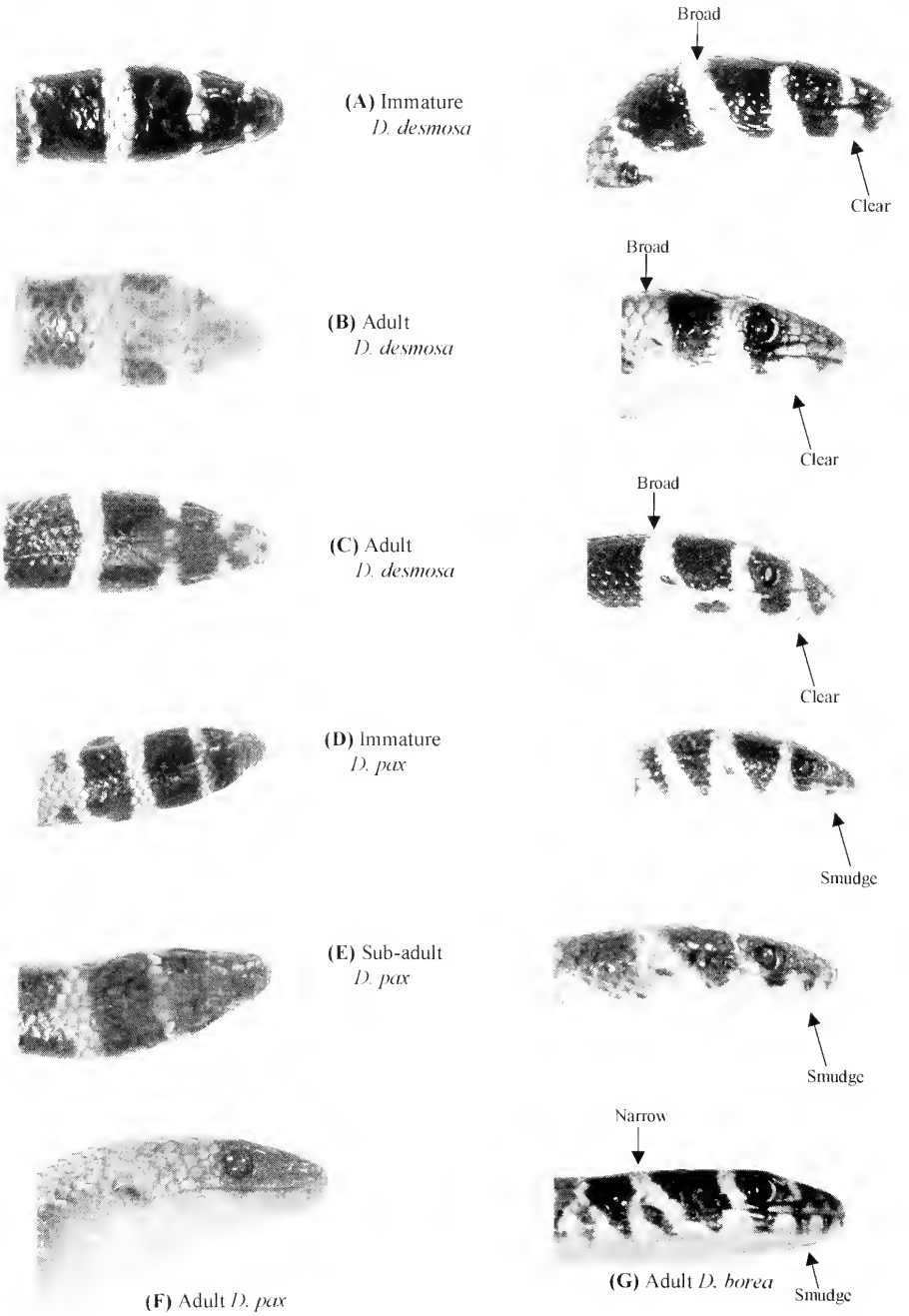


Figure 12 Head patterning of A, *D. desmosa*, immature from Townsend Ridges (151252), B, *D. desmosa* adult with weak bands forward of eyes from Staffords Bore (64097), C, *D. desmosa* adult with strong bands from Ayers Rock, Northern Territory (NTM 34489), D, *D. pax* immature from 82km E Port Hedland (140396), E, *D. pax* sub-adult with fading bands from DeGrey River Station (132549) and arrows indicating clear or pigmented suture and broad auricular band in *D. desmosa*, all shown in dorsal and lateral views and F, *D. pax* adult from Potter Island (139353) showing complete lack of head patterning, G, *D. borea* adult with strong bands from Mitchell Plateau (77201) and arrows indicating pigmented suture and narrow auricular band, shown in lateral views.

139062-63) where *D. desmosa* (e.g., 139089) is also recorded. Currently this represents the only known instance of sympatry for these two species in Western Australia. However, the single specimen of *D. desmosa* was obtained on the crest of a *Triodia*-covered sandridge, while specimens of *D. borea* came from the edge of a spring with *Melaleuca leucadendra* on clayey soil. Records of *D. desmosa* and *D. borea* from the arid southern Northern Territory and northwestern South Australia also tend to come from different localities. Systematic faunal surveys have only recently recorded *D. borea* from northwestern South Australia (Robinson *et al.* 2003) and the Uluru National Park (McAlpin 2005). Generally, *D. borea* prefers areas of stony or heavy soils with *Triodia* and tussock grasses or savanna woodland with grass/leaf litter (B. Maryan, *personal observation*) and appears to not occupy *Triodia* on sandplains (Kluge 1974: 82), the preferred habitat of *D. desmosa*. The available information thus suggests a degree of habitat partitioning between *D. desmosa* and *D. borea* in areas where their ranges interdigitate.

In Western Australia, other recorded instances of sympatry involving *D. desmosa* include *D. haroldi* and *D. nasuta* in the Little Sandy Desert and Central Ranges (B. Maryan and P. Doughty, *personal observation*) and *D. butleri* has been collected from the Officer Basin area, where *D. desmosa* (e.g., 145073) is also recorded. In the Northern Territory, Reid *et al.* (1993) records both *D. butleri* and *D. nasuta* from the same survey site as *'D. pax'* (= *D. desmosa*) in Uluru National Park.

Comparison with other species

Delma desmosa will be compared first with *D. pax* and *D. borea*, two species with which it has previously been confused, and then with other regionally sympatric *Delma* spp.

Delma pax and *D. desmosa* are similar in body proportions (Table 1) and agree in most details of head and body scalation. The head pattern of juveniles is also similar, consisting of four 'opalescent' black bands and pale interspaces (Figure 12A, D), but the fate of this pattern is very different. In *D. desmosa* the bands are retained through to adult life (Figures 10, 12C) while in *D. pax* they undergo pronounced ontogenetic fading (Figure 12E) such that adults typically lack any head pattern (Figures 12F, 14). Another difference in head pattern concerns the ventral extent of the anterior dark head bands; in *D. pax* the first (on snout) and second (through eyes) bands typically terminate on the infralabials, while in *D. desmosa* they extend onto the mental scale and below the infralabials, and are visible in ventral view. In addition, the first dark head band on the snout in *D. pax* is regularly weak or absent and usually distinct in *D. desmosa*. Immature specimens of *D. pax* typically have three dark brown smudges on the lower lip, situated over the sutures between the mental and anterior two infralabial scales (Figure 12D–E). In *D. desmosa* the suture between the first and second infralabial typically is unpigmented (Figure 12A–C).

On meristic and mensural data, *D. desmosa* averages slightly smaller than *D. pax* for most measurements (Table 1). This contrast is particularly striking for males, reflecting more pronounced sexual dimorphism in *D. pax* than *D. desmosa* (Table 1). In both sexes the mean ventral scale count is significantly lower in *D. desmosa* than in *D. pax* (Table 4).

Delma borea is similar to *D. desmosa* in overall body size but has shorter hindlimb flaps and a significantly higher average number of ventral scales in both sexes (Tables 1, 4). The two species are readily distinguished by head pattern. *Delma borea* has a pale inter-band on the back of head which narrows dorsally but broadens or 'forks' at the ear aperture (Figure 12G). In *D. desmosa* the auricular inter-band typically is of even width or only slightly broader laterally (Figure 12A–C). Most *D. borea* also have some variegated ventrolateral scales on the forebody. These scales are unpatterned in *D. desmosa*. *Delma borea* typically have the fourth supralabial positioned below the eye (typically the third in *D. desmosa*).

Delma borea and *D. pax* both have three dark brown smudges situated between the nostril and the eye, and positioned over the mental and infralabial scale sutures (Figure 12D–E, G). These smudges are absent only in some adults devoid of any head pattern (Figure 12F). In contrast, the suture between the first and second infralabial typically is clear in *D. desmosa*; in occasional specimens (e.g., 140442) the first head band completely covers the upper portion of the first infralabial scale.

Apart from *D. borea*, the only *Delma* species with distributions overlapping that of *D. desmosa* are *D. butleri*, *D. haroldi*, *D. nasuta* and *D. tincta*. *D. desmosa* is easily distinguished from the first three by having dark dorsal head markings and from *D. tincta* by the presence of two pairs of supranasal scales (one pair in *D. tincta*), a higher midbody scale row count (modally 16 versus 14) and unpatterned ventrolateral scales on the forebody.

Habitat

The holotype was raked (using a 3-prong cultivator) from *Eucalyptus chippendalei* leaf litter in dune swale on red sand with groundcover of *Thryptomene* and *Triodia* (Figure 13). Notes accompanying some Western Australian paratypes include "raked from dead *Triodia* clumps and shrubs on crest of sandridges" (e.g., 88535-41); "pit-trapped on claypan with *Acacia* over mixed grasses

Figure 13 *Triodia* sandplain in swale with red sand dune covered with *Eucalyptus chippendalei, Acacia* and *Triodia* at the Little Sandy Desert WA, the habitat for *Delma desmosa* (B. Maryan).

and samphire" (e.g., 75798); "along minor drainage lines with fringing *Eucalyptus*" (e.g., 63313, 94776-77) and "active at night on road in sandplain with sparse *Acacia* over *Triodia*" (e.g., 114555). Habitat details for paratypes from Northern Territory and northwestern South Australia are "pit-trapped in *Triodia* grassland" (e.g., 14901, 15038, 15138, 15144, 15146, 15151, 15230, 15501, 20250); "mulga woodland over bluebush and tussock grasses on sandplain" (e.g., 48671) and "under loose stones on rocky hillside" (e.g., 59561).

Remarks

The specific characteristics of *D. desmosa* have created prior confusion between *D. borea* and *D. pax*. Shea (1991) drew attention to this problem by mentioning a specimen from Ayers Rock (NTM 1319; renumbered 34489) that shares *D. borea* and *D. pax* scalation characters. This specimen is herein referred to *D. desmosa* (Figure 12C). Systematic faunal surveys by Reid *et al.* (1993) and McAlpin (2005) also mentioned problems with identification and variously assigning a *Delma* sp. to *D. borea* or *D. tincta* in previous reports, but identified by them as '*D. pax*'. Their accounts of '*D. pax*' from Uluru National Park are most likely based on individuals of *D. desmosa*.

Ehmann (1992: 94) and Reid *et al.* (1993: 49) illustrate *D. desmosa* from the Great Sandy Desert, Western Australia and from Uluru National Park, Northern Territory respectively; in both publications the specimens are identified as *D. pax*.

Delma pax Kluge, 1974

Figure 14

Delma pax Kluge (1974: 113–117). 14804 in the Western Australian Museum, an adult female collected on 21 May 1961 by G.M. Storr at Jones River, Western Australia (20°58'S, 117°23'E).

Revised diagnosis

A moderately small, stout species of *Delma* (SVL up to 98mm) with modally 16 midbody scales, two pairs of supranasals, and a plain adult colouration due to pronounced ontogenetic fading of dorsal head markings (markings prominent in juveniles).

Description

Rostral with obtuse apex, penetrating between rostral supranasals; two pairs of supranasals, caudal pair much larger; rostral supranasals in moderate contact with first supralabial and caudal supranasals in point contact or only narrowly separated from the nostril; postnasal single; loreals 4–10, subequal; suboculars 2–4; supraciliaries 5 (rarely 4), fifth much larger; supraoculars 2, second wider than first; supralabials 5–6, third typically elongate and positioned below eye (occasionally, fourth is below eye), posteriormost supralabial much smaller; infralabials 4, third elongate; occipital present; upper temporals 2. Midbody scale rows usually 16 [14 in 12.4 % of specimens; 18 in one specimen (119045; from Port Hedland)]; specimens with 14 midbody scale rows are Bohemia

Figure 14 Adult *Delma pax* from Meentheena, photographed in life (B. Maryan).

scattered throughout the range of *D. pax* and often come from the same localities as specimens with 16 midbody scale rows. Storr *et al.* (1990) state that *D. pax* has 'rarely 17' midbody scale rows but without citing specimen details. Transversely enlarged ventral scales 50–60; hindlimb scales 8–10.

Morphological Variation: Kluge (1974) examined 16 *D. pax* and recorded only a single specimen with the fourth supralabial below the eye on one side only (SAM 3445 from Pilgangoora Well). Our examination of a further 97 specimens found this condition in unilateral or bilateral states in 20% of individuals, as follows: fourth supralabial below eye on both sides in 73146, 102137, 113387, 119045-046, 129930, 132657, 135919, 139294, 140396, 145680 and 146649; fourth supralabial below eye on right side only in 127829, 135320, 139353 and 146591, on left side only in 9943, 73841 and 129658.

Other variants are:

9946 has fusion of second and third supraciliaries (total 4) on both sides; 132606 has same condition on right side only.

81390 has rostral contacting caudal supranasals and thus separating rostral supranasals; 129930 has small scale interposed between rostral supranasals.

119045 has two upper loreal scales on right side.

145748 has rostral and caudal supranasals fused on right side.

Colouration and patterning

In preservative, upper and lateral surface brown to reddish brown merging into pale grey on lower lateral surfaces. Lateral scales on forebody are plain. Lower surface white and unpatterned.

Head of juveniles typically with strong pattern of transverse bands (Figure 12D). Intensity of bands diminishes with increasing body size (= age) such that head and neck of large adults are typically light to reddish brown and unpatterned (Figures 12F, 14). Where traces of pattern are retained (e.g., 129658, 132548, 139170, 140021), this consists of very diffuse pale brown spaces ('ghosting' of bands) between the ears and behind the eyes.

Head pattern of immature specimens consists of three to four brown to blackish brown bands that narrow as they descend and terminate obtusely on the infralabials and behind the ear. The first band (on snout) is variably developed and may be absent, even on juveniles. The bands crossing the back of the head and the neck are broader and more distinct and the pale interbands are typically of even width, without any lateral widening. The interband spaces are pale reddish brown in life but this typically fades to a lighter brown or a greyish-white (e.g., 140396) in preservative. A narrow and faint pale band is usually present on the neck behind the posteriormost dark band; this is, occasionally followed on the side of the neck by a narrow dark band (e.g., 140396).

Supralabials and infralabials of juveniles whitish in between dark bands. Dark bands extend below mouth and terminate on suture lines between mental and first infralabial scales, between second and third infralabials, and between third and fourth

infralabials. These suture line smudges undergo ontogenetic fading in concert with the general head pattern.

Distribution and sympatry

Widespread throughout Pilbara region of Western Australia (Figure 8) with southerly extension to northern Gascoyne at Turee Creek, extending north to DeGrey River Station, east to Carawine Gorge and 30km east of Newman and southwest to Mount Minnie and Cane River Stations. Also occurs on Potter Island off Pilbara coast. Endemic to Western Australia.

As noted earlier, *D. pax* appears to be allopatric with respect to the closely related *D. desmosa* (Figure 8). However, *D. pax* is regionally sympatric in the Pilbara region with *D. butleri, D. haroldi, D. elegans* Kluge, 1974, *D. nasuta* and *D. tincta*. Recorded instances of sympatry involving *D. pax* include *D. haroldi, D. nasuta* and *D. tincta* from multiple localities throughout the Pilbara region. For instance, in the vicinity of Port Hedland, *D. pax, D. haroldi* and *D. tincta* have all been observed crossing the same section of sealed road at night. *Delma pax* and *D. nasuta* were observed together in the same context in the vicinity of Newman (B. Maryan and B. Bush, *personal observation*). *Delma pax* also has been recorded with *D. elegans* from several localities including Meentheena and Pannawonica.

Comparison with other species

Delma pax will be compared first with *D. borea*, and then with other regionally sympatric *Delma* spp. For comparison with *D. desmosa* see the preceding account.

Both sexes of *D. pax* average larger than *D. borea* in almost all linear measurements (Tables 1, 4), while average ventral scale counts are significantly higher in female *D. pax* than female *D. borea* but not in males. Body pattern in *D. pax* features plain ventrolateral scales on the forebody, whereas *D. borea* typically has variegated scales in this area. Specimens of *D. pax* that retain traces of the immature head pattern (Figure 12E) are distinguished from *D. borea* by having a band on back of head that is slightly broader and of more even width (in *D. borea* the auricular band is narrower mid-dorsally but broadens laterally, often 'forking' at the ear aperture; Figure 12G). *Delma pax* typically have the third supralabial positioned below the eye (typically the fourth in *D. borea*).

As indicated above, five other *Delma* species occur in regional sympatry with *D. pax* (*D. butleri, D. haroldi, D. elegans, D. nasuta* and *D. tincta*). The relatively inornate *D. butleri* bears a superficial resemblance to adult *D. pax* but differs in having more complex patterning on the lips, side of head and neck (variably marked with brown and white spots, blotches or vertical streaks). *Delma haroldi* is more distinct with narrow wavy pale bands (but no dark bands) across the head and neck. *Delma elegans* has five or six dark head bands that descend obliquely forward and also has higher midbody scale row counts (modally 18 versus 16). *Delma nasuta* has a longer, sharper snout with a spotted or reticulated pattern on the dorsal and ventral surfaces. Finally, *D. tincta* has one pair of supranasals (versus two in *D. pax*), lower midbody scale row counts (modally 14 versus 16), fewer loreal scales on average (Table 1) and variegated scales on the lateral forebody (versus plain scales in *D. pax*). *Delma tincta* generally averages smaller than *D. pax* in linear dimensions (Table 1).

Habitat

Delma pax occupies a variety of habitats in the Pilbara region including sandy riverside flats and stony slopes with heavy soils. It is most frequently obtained from *Triodia* clumps but also shelters in flood debris along dry watercourses. The species is often observed at night active on sealed roads (B. Maryan, *personal observation*).

Remarks

Kluge (1974: 116–117) illustrates the head region of both immature and adult *D. pax*. Adult *D. pax* is illustrated by Wilson and Knowles (1988: 249), Storr *et al.* (1990: Plate 17.3), Cogger (2000: 290) and Wilson and Swan (2003: 117). Wilson and Swan (2003: 111) illustrate an immature *D. pax* (140396) from the Port Hedland district, mislabeled as *D. borea*.

Remarks on the distribution of *Delma borea*

The taxonomic changes proposed above also help clarify the species limits and geographic distribution of *D. borea*. As delimited here, *D. borea* in Western Australia is a moderately small, stout species of *Delma* (SVL up to 98mm) with modally 16 (rarely 17) midbody scales, two pairs of supranasals, the fourth supralabial scale positioned below the eye (unilaterally third supralabial below eye in two out of 114 specimens), and variegated ventrolateral scales on forebody. Juveniles possess well-defined dark head bands. Adults undergo ontogenetic fading to varying degree and usually possess indistinct pale brown bands on the head and neck. These morphological characteristics are consistent with previous accounts of *D. borea* in the more easterly parts of its range (Kluge 1974).

Figure 15 shows the distribution of *D. borea* in Australia, based on our reassessment of specimens in the collection of the Western Australian, Northern Territory and South Australian Museums. In Western Australia, this species ranges from the Kimberley southwest to Mandora inland of the 80 mile beach, and south to the Edgar Ranges, 25 km E

Downs and Denison Range. It is present on numerous islands off the Kimberley coast (Troughton, Naturalist, Coronation, Heywood, Sunday, Augustus, King Hall, Cockatoo and Koolan) and at least three islands off the Pilbara coast (Barrow, Hermite and Rosemary). It also occurs in the Northern Territory, western Queensland and northwestern South Australia (Kluge 1974; Shea 1987, 1991; Ingram and Raven 1991; Ehmann 2005). In the Northern Territory, *D. borea* is most common in the Top End, with the southernmost records at Wave Hill, Helen Springs and 50 km S MacArthur River camp (Shea 1991); it appears to be sparsely distributed south of the 20° parallel that includes its occurrence in northwestern South Australia on Aboriginal Lands (Ehmann 2005). Kluge's (1974: Figure 47) map for this species shows a record in northwestern South Australia but without an equivalent specimen listed under Paratypes; we assume that the map is in error.

Three specimens included by Kluge (1974: 192) within *D. borea* warrant special mention. Specimen 25201 from 32 km E Jiggalong was also mapped as *D. borea* by Storr *et al.* (1990) and further cited by Shea (1991) as representing this taxon. This specimen is confirmed here as a member of the *D. tincta* group due to the presence of a enlarged upper temporal scale bordering each parietal. It differs from each of *D. borea* and from *D. desmosa* in being more slender bodied, and differs from *D. desmosa* in having more pronounced variegation of the ventrolateral scales on the forebody. In both of these respects, the specimen resembles *D. tincta*. However, it differs from *D. tincta* in having paired supranasals and 16 midbody scale rows, and in these respects, more closely resembles *D. borea* and *D. desmosa*. This specimen might represent an outlier of *D. borea*, a somewhat aberrant *D. desmosa*, or another, as yet unrecognized taxon.

Specimen SAM 5058 referred to *D. borea* also by Shea (1991) from the Warburton Range is similar in most respects to specimen 25201. The colour pattern is similar to both *D. borea* and *D. tincta*, most notably in the presence of variegated ventrolateral scales on the forebody. The specimen has two pairs of supranasal scales and the fourth supralabial positioned bilaterally below the eye, both features shared with typical *D. borea*. However, it is slender

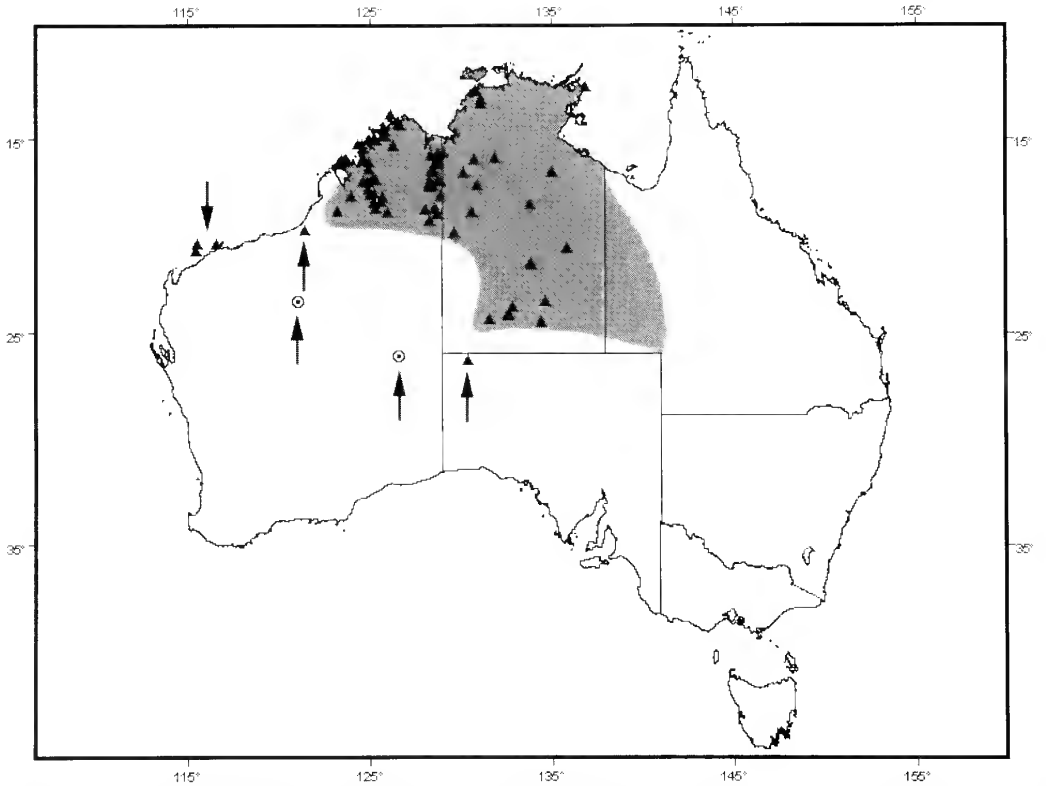


Figure 15 Map of Australia showing distribution of *D. borea* (shading) and location of specimens examined in this study (triangles). Arrows indicate outlier populations at Mandora, western Pilbara islands and northwestern South Australia and the two specimens (circles with cross) from 32 km E Jiggalong and Warburton Range that are regarded as *D.* sp. *incertae sedis* pending further field survey and analysis.

bodied and has 14 midbody scales, more typical of *D. tincta*. The presence of variegated ventrolateral scales on the forebody and the absence of strong head patterning distinguish the specimen from regionally sympatric *D. desmosa*. The desert regions are poorly sampled for herpetofauna (How and Cowan 2006) and until further material is available, we recommend that the Warburton Range and Jiggalong populations be treated as *Delma* sp. *incertae sedis*.

Specimen SAM 4475 from Tambrey is listed twice by Kluge (1974: 192), once as a paratype of *D. borea* and again as a paratype of *D. elegans*. Advice from the South Australian Museum indicates that there have been no changes made in relation to this registration number which is currently attached to a paratype of *D. elegans* (M. Hutchinson, *personal communication*); the duplicate listing under *D. borea* is assumed to be an editorial error.

DISCUSSION

Taxonomic diversity of the *Delma tincta* group

The present study has identified two additional members of the *Delma tincta* group as defined by Shea (1991). *Delma desmosa* from the arid sand deserts of western and central Australia is a close relative of *D. pax* which is now recognized as endemic to the Pilbara region. The ranges of *D. pax* and *D. desmosa* appear to be allopatric or parapatric (current records suggest a gap of no more than 90 km between populations). These species are weakly differentiated genetically and they differ morphologically mainly in features of colouration (most notably the degree of ontogenetic fading of the juvenile head markings), and in the degree to which sexual dimorphism is expressed. However, the fact that an abrupt boundary is maintained between the two taxa over a very large distance around the periphery of the Pilbara uplands indicates that they represent discrete evolutionary lineages, each with its own set of ecophysiological requirements, and thus warrant specific recognition. Gene flow between the populations, if it occurs at all, is clearly limited and insufficient to influence the genetic or morphological characteristics of the spatially adjacent populations. Nevertheless, contact zones between *D. pax* and *D. desmosa* should be sought in which to investigate the nature and extent of genetic interactions between these taxa. Furthermore, ecological and behavioural comparisons of these closely related species might yield valuable insights into the adaptive significance of head patterning in *Delma*.

Delma tealei, an endemic of the Cape Range Peninsula, is most similar morphologically to *D. borea* and to a lesser extent, to *D. tincta*, all three taxa sharing the unusual characteristic of variegated scales on the ventrolateral forebody. The allozyme data suggest a possible sibling relationship between *D. borea* and *D. tealei*, and a more remote association with *D. tincta*. However, the level of divergence is much greater than that observed between *D. pax* and *D. desmosa*, and identifies *D. tealei* as a well established lineage within the *D. tincta* group.

Biogeography of the *Delma tincta* group

The *D. tincta* group as a whole has a 'Torresian' distribution (sensu Cogger and Heatwole 1981). This appears to be unique within the genus *Delma*, since other species groups recognized on morphological (Kluge 1974; Shea 1991) or molecular criteria (Jennings *et al.* 2003) have geographic distributions that either range across southern Australia (*D. australis* + *D. torquata* Kluge, 1974; *D. fraseri* + *D. grayii*; *D. petersoni* + *D. inornata*), are confined to eastern Australia (*D. impar* + *D. molleri* + *D. mitella* Shea, 1987), or are centred on the arid inland region (*D. butleri/D. haroldi* + *D. nasuta*). With a total of five species, the *D. tincta* group is also the most speciose of the major intrageneric lineages identified to date. However, as noted above, this may reflect a lack of complete taxonomic discrimination in some other groups, most notably in the *D. butleri/D. haroldi* complex and in the *D. australis* group (Aplin and Smith 2001).

Within the *Delma tincta* group, the widely distributed *D. tincta* appears to be broadly sympatric with each of *D. borea*, *D. pax* and the two additional members described in this paper. Whether this entails instances of true syntopy is not known. However, in our view the likelihood of syntopy is enhanced by the unusual morphological characteristics of *D. tincta* within this group, in particular its relatively small adult size and slender build (as reflected by a reduced number of midbody scale rows). *Delma tealei*, which is at least regionally sympatric with *D. tincta* on the Cape Range Peninsula, shares several of these characteristics and it would be of great interest to know more about the ecological interaction between these species.

Delma pax and *D. desmosa* have allopatric or parapatric distributions, the former confined to the Pilbara region, and the latter found in the surrounding sandy deserts and extending east into the central Australian deserts. Along its northern margin, the range of *D. desmosa* appears to interdigitate with that of *D. borea* but with no records of syntopy. These taxa differ in relatively subtle aspects of body colouration, meristics and in relative hindlimb flap length, and they may be weakly differentiated ecologically and subjected to mutual competitive exclusion. Somewhat surprisingly, given the high degree of

morphological similarity, *D. desmosa* and *D. borea* are well-differentiated genetically.

The ranges of *D. borea* and *D. pax* approach regional sympatry in northwestern Australia. *Delma pax* is restricted to the mainland Pilbara region where it occupies a variety of local habitat types being only recently recorded on Potter Island off the Pilbara coast. *Delma borea*, in contrast, is present on several of the western Pilbara islands. On Barrow Island it is found together with *D. nasuta* and *D. tincta* and on Hermite Island it is recorded with *D. nasuta* (Burbidge *et al.* 2000).

The disjunct occurrence of *D. borea* in northwestern Australia begs explanation. The flora and fauna of Barrow and Hermite Islands off the Pilbara coast are closely allied with those of the Cape Range Peninsula (Keighery and Gibson 1993; Baynes and Jones 1993; Kendrick 1993), reflecting not only the geological similarity between the two areas (both are anticlinal structures comprised of Miocene limestones) but also that during periods of lowered sea level through the late Pliocene and Pleistocene, both formed rocky plateaux on a sandy, emergent continental shelf. Despite this overall similarity, the Pilbara islands host a number of 'northern monsoonal' faunal elements that are absent from the Cape Range Peninsula. One of these is *D. borea*, perhaps replaced on the peninsula by the morphologically similar *D. tealei*. Others include a murid rodent *Pseudomys nanus* (Gould, 1858) and a skink *Ctenotus angusticeps* Storr, 1988. Another 'northern monsoonal' mammal species, the Northern Nailtail Wallaby *Onychogalea unguifera* (Gould, 1841), is represented in an early Holocene subfossil assemblage from the Montebello islands (Veth 1993). These taxa are typically associated either with grassland communities on coastal plains (*P. nanus* and *O. unguifera*) or with coastal samphire communities (*C. angusticeps*), vegetation types that were most likely broadly continuous along the emergent northwestern continental shelf during periods of lower sea level. The present distribution of *D. borea* suggests that it, too, was a member of this now emergent continental shelf community that survives in relictual form only on the Pilbara islands.

Molecular clock estimates suggest a staggered origin of the major species group lineages within *Delma* during the early to mid-Miocene, around 20–28 million years ago (Jennings *et al.* 2003). The *Delma tincta* group probably arose during the latter part of this radiation. Divergence of the modern species lineages (*D. pax, D. tincta, D. borea*) probably occurred during the late Miocene (ca. 8–9 million years ago). Other speciation events in *Delma* typically are of similar or even greater antiquity, if the molecular clock estimates are accepted as valid (Jennings *et al.* 2003).

Delma tealei shows a similar level of genetic differentiation to the other previously recognized members of the *D. tincta* group and thus may also have originated during the late Miocene. This corresponds closely to the time of emergence of the Cape Range (Wyrwoll *et al.* 1993) and it is tempting to link the two events via a dispersal or vicariance event. However, the probable great antiquity of the *D. tealei* lineage (as indicated by its genetic distinctiveness) leaves open the possibility that *D. tealei* was formerly more widespread under the very different bioclimatic regime of the late Tertiary period and is relictual on Cape Range Peninsula. *Delma desmosa*, in contrast, is genetically close to its sibling *D. pax* and these taxa probably diverged during the late Pliocene or Pleistocene (i.e., within the last 2–3 million years). In broad terms, this corresponds to the period of progressive desertification of Australia (White 1994; Fujioka *et al.* 2005) and it seems likely that this later period of diversification within the *D. tincta* group occurred in response to the emergence of new kinds of arid zone habitats.

Species identification in *Delma* and a new dichotomous key

As noted in the Introduction, this study was initiated in response to seemingly anomalous identifications of Pilbara *Delma* specimens obtained through application of the key published in Storr *et al.* (1990: 114). In most cases, this confusion involved individuals of *D. pax* or *D. desmosa* in which the third supralabial scale is divided unilaterally or bilaterally, thereby leading to ambiguity at the second key couplet in which the relationship of supralabial scales to the eye is used. Similar difficulties were also encountered as a consequence of intraspecific variation in other 'diagnostic' characters within the genus *Delma*, including the condition of the supranasal scales, the number of midbody scale rows and aspects of head patterning. Fundamentally, these difficulties reflect the fact that the genus *Delma* is speciose yet morphologically conservative. Moreover, problems of identification are compounded by marked ontogenetic transformations in head pattern that occur in some species of *Delma* but not in others.

In conclusion, we offer a revised dichotomous key to the *Delma* species of Western Australia. Given the difficulties in accurate identification of this group, we suggest that the key be used only as a first step towards taxonomic identification of adult specimens, which should then be confirmed by direct comparison with voucher material or through genetic analysis. Moreover, if possible, we recommend that the following conditions be met prior to application of the key: 1) that the stage of sexual maturity of individual animals is determined; 2) that 'typical' scalation characters are determined

through examination of locally obtained series rather than individual specimens; and 3) that close attention is paid not only to the small number of standard diagnostic features employed in the key but also to subtleties of head and body scale patterning within regional *Delma* assemblages.

Key to Western Australian *Delma*

1. Typically one pair of supranasals 2
   Typically two pairs of supranasals 3
2. Smaller (SVL up to 57mm); typically 18 midbody scale rows; side of neck and forebody usually finely barred with black; no broad dark bands across head and neck ..... *australis*
   Longer (SVL up to 92mm); typically 14 midbody scale rows; side of forebody usually with variably coloured scales; broad dark bands across head and neck (often fade with age) ..... *tincta*
3. Typically third supralabial below the eye; typically 14 midbody scale rows; Cape Range Peninsula ..... *tealei*
   Either third or fourth supralabial below the eye; between 16–20 midbody scale rows 4
4. Typically third (occasionally fourth) supralabial below the eye 5
   Typically fourth supralabial below the eye 6
5. Dark bands across head and neck persistent at all ages; two dark smudges on infralabials below lores; deserts ..... *desmosa*
   Dark bands across head and neck absent in adults; three dark smudges on infralabials below lores; Pilbara ..... *pax*
6. Typically 16 midbody scale rows 7
   Typically 18 midbody scale rows 8
7. Throat white; Kimberley and some Pilbara islands ..... *borea*
   Throat with fine dark variegations; southwest of WA ..... *fraseri*
8. Dark bands across head and neck descend obliquely forwards, terminating acutely; Pilbara ..... *elegans*
   Dark bands run straight across head and neck and meet to form black bands across the chin and throat; southern Great Victoria Desert ... . *petersoni*
9. Narrow, wavy pale bands across head and neck ..... *haroldi*
   No pale bands across head and neck 10
10. Side of forebody with numerous pale vertical streaks or bars; lower surface yellow ... *grayii*
    Side of forebody without numerous pale vertical streaks or bars; lower surface white with or without dark markings 11
11. Snout long; dorsal scales spotted and flecked with dark brown; ventral scales usually dark-edged ..... *nasuta*
    Snout short; dorsal scales finely dark-edged; ventral scales without dark edges ..... *butleri*

ACKNOWLEDGEMENTS

This study would not have been possible without financial support for the genetic examinations from Methanex Australia Pty. Ltd. R. How, P. Doughty and C. Stevenson of the Western Australian Museum provided support and assistance during the study. We are grateful to R. O'Shea formerly of the Western Australian Museum for doing the head drawings and taking photographs of preserved specimens. L. Schmitt of the University of Western Australia kindly provided statistical advice. P. Horner and G. Dally of the Northern Territory Museum, M. Hutchinson and C. Secombe of the South Australian Museum and R. Sadlier of the Australian Museum kindly allowed access to specimens. G. Shea, M. Hutchinson and P. Doughty offered insightful comments of the manuscript.

Thanks also to the many field herpetologists in Western Australia who have made substantial contributions to the *Delma* collection of the Western Australian Museum, most notably D. Algaba, B. Bush, R. Browne-Cooper, G. Harold, P. Kendrick, D. Pearson, D. Robinson and R. Teale.

REFERENCES

Adams, M., Baverstock, P.R. and Reardon, T. (1987). Electrophoretic resolution of species boundaries in Australian Microchiroptera. I. *Eptesicus* (Chiroptera, Vespertilionidae). *Australian Journal of Biological Sciences* **40**: 143–162.

Aplin, K.P. (1998). Three new blindsnakes (Squamata: Typhlopidae) from northwestern Australia. *Records of the Western Australian Museum* **19**: 1–12.

Aplin, K.P. and Smith, L.A. (2001). Checklist of the frogs and reptiles of Western Australia. *Records of the Western Australian Museum* Supplement No. 63: 51–74.

Baynes, A. and Jones, B. (1993). The mammals of Cape Range peninsula, north-western Australia. Pp. 207–225 in W.F. Humphreys (ed.) *The Biogeography of Cape Range, Western Australia. Records of the Western Australian Museum* Supplement No. 45.

Burbidge, A.A., Blyth, J.D., Fuller, P.J., Kendrick, P.G., Stanley, F.J. and Smith, L.A. (2000). The terrestrial vertebrate fauna of the Montebello Islands, Western Australia. *CALM Science* **3**: 95–107.

Cogger, H.G. and Heatwole, H. (1981). The Australian reptiles: Origins, biogeography, distribution patterns

and island evolution. Pp 1331–1373 in *Ecological biogeography of Australia* (A. Keast ed.) Dr W. Junk, The Hague.

Cogger, H.G. (2000). Reptiles and Amphibians of Australia. Reed New Holland, Frenchs Forest, NSW.

Ehmann, H. (1992). Encyclopedia of Australian Animals. Reptiles. Angus & Robertson, Sydney.

Ehmann, H. (2005). South Australian Rangelands and Aboriginal Lands Wildlife Management Manual. Department of Water, Land and Biodiversity Conservation, South Australia.

Felsenstein, J. (1993). PHYLIP (Phylogeny Inference Package. Version 3.5c). Distributed by the author, University of Washington, Seattle.

Fujioka, T., Chappell, J. Honda, M., Yatsevich, I., Fifield, K. and FAbel, D. (2005). Global cooling initiated stony deserts in central Australia 2–4 Ma,dated by cosmogenic 21Ne-10Be. *Geology* **33**: 993–996.

How, R.A. and Cowan, M.A. (2006). Collections in space and time: geographical patterning of native frogs, mammals and reptiles through a continental gradient. *Pacific Conservation Biology* **12**: 111–133.

Ingram, G.J. and Raven, R.J. (1991) eds. An atlas of Queensland's Frogs, Reptiles, Birds and Mammals. Queensland Museum.

Jennings, W.B., Pianka, E.R. and Donnellan, S. (2003). Systematics of the Lizard Family Pygopodidae with Implications for the Diversification of Australian Temperate Biotas. *Systematic Biology* **52**: 757–780.

Keighery, G. and Gibson, N. (1993). Biogeography and composition of the flora of the Cape Range peninsula, Western Australia. Pp. 51–85 in W.F. Humphreys (ed.) *The Biogeography of Cape Range, Western Australia. Records of the Western Australian Museum* Supplement No. 45.

Kendrick, P.G. (1993). Biogeography of the vertebrates of the Cape Range peninsula, Western Australia. Pp. 193–206 in W.F. Humphreys (ed.) *The Biogeography of Cape Range, Western Australia. Records of the Western Australian Museum* Supplement No. 45.

Kluge, A.G. (1974). A taxonomic revision of the lizard family Pygopodidae. *Miscellaneous Publications of the Museum of Zoology, University of Michigan* No. 147: 1–221.

Kluge, A.G. (1976). Phylogenetic relationships in the lizard family Pygopodidae: An evaluation of theory, methods and data. *Miscellaneous Publications of the Museum of Zoology, University of Michigan* No. 152: 1–72.

McAlpin, S. (2005). Uluru – Tjuta National Park Vertebrate Fauna Resurvey: 2004. Consultancy Report to Parks Australia North. The author, Lismore.

Page, R.D.M. (1996). TREEVIEW: An application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* **12**: 357–358.

Reid, J.R.W., Kerle, J.A. and Morton, S.R. (1993). Uluru Fauna. The Distribution and Abundance of Vertebrate Fauna of Uluru (Ayers Rock-Mount Olga) National Park, N.T. Australian National Parks and Wildlife Service series – Kowari, Canberra.

Richardson, B.J., Baverstock, P.R. and Adams, M. (1986). Allozyme Electrophoresis: A Handbook for Animal Systematics and Population Studies. Academic Press, Sydney.

Robinson, A.C., Copley, P.B., Canty, P.D., Baker, L.M. and Nesbitt, B.J. (2003). A biological survey of the Anangu Pittjantjatjara Lands South Australia. South Australian Department for Environment and Heritage, Adelaide.

Shea, G.M. (1987). Two new Species of *Delma* (Lacertilia: Pygopodidae) from northeastern Queensland and a Note on the Status of the Genus *Aclys*. *Proceedings of the Linnean Society of New South Wales* **109**: 203–212.

Shea, G.M. (1991). Revisionary notes on the genus *Delma* (Squamata: Pygopodidae) in South Australia and the Northern Territory. *Records of the South Australian Museum* **25**: 71–90.

Smith, L.A. and Adams, M. (2006). Revision of the *Lerista muelleri* species-group (Lacertilia: Scincidae) in Western Australia, with a redescription of *Lerista muelleri* (Fischer, 1881) and the description of nine new species. *Records of the Western Australian Museum* (in press).

Storr, G.M. (1987). Three new legless lizards (Pygopodidae) from Western Australia. *Records of the Western Australian Museum* **13**: 345–355.

Storr, G.M. and Hanlon, T.M.S. (1980). Herpetofauna of the Exmouth Region, Western Australia. *Records of the Western Australian Museum* **8**: 423–439.

Storr, G.M., Smith, L.A. and Johnstone, R.E. (1990). Lizards of Western Australia. III Geckos & Pygopods. Western Australian Museum.

Storr, G.M., Smith, L.A. and Johnstone, R.E. (2002). Snakes of Western Australia. Revised Edition. Western Australian Museum.

Veth, P. (1993). The Aboriginal occupation of the Montebello Islands, north-west Australia. *Australian Aboriginal Studies* **24**: 81–89.

White, M.E. (1994). After the greening, the browning of Australia. Kangaroo Press, Kenthurst, Australia.

Wilson, S.K. and Knowles, D.G. (1988). Australia's Reptiles. A photographic reference to the Terrestrial Reptiles of Australia. Collins, Sydney.

Wilson, S.K. and Swan G. (2003). A Complete Guide to Reptiles of Australia. Reed New Holland, Frenchs Forest, NSW.

Wyrwoll, K.-H., Kendrick, G.W. and Long, J.A. (1993). The geomorphology and Late Cenozoic geomorphological evolution of the Cape Range – Exmouth Gulf region. *In* W.F. Humphreys (ed.) *The Biogeography of Cape Range, Western Australia. Records of the Western Australian Museum* Supplement No. 45: 1–23.

Manuscript received 9 November 2005; accepted 10 November 2006

APPENDIX 1

Lists of Specimens examined

Legend for Museum registration numbers: WAM = Western Australian Museum; NTM = Northern Territory Museum; SAM = South Australian Museum.

Delma borea Kluge 1974
SAM: 42018-20, 42046, 42189 2 km W Hanging Knoll (26°19'23"S 130°23'36"E).
NTM: 1317 Barrow Creek (21°31'S 133°53'E); 1574 Tanami Bore (19°58'S 129°40'E); 5371 Barrow Creek (21°31'S 133°53'E); 5824-25, 6516-6517, 6610 Wave Hill (17°29'S 130°57'E); 6594 70 km N Top Springs (16°00'S 131°56'E); 9133 Keep River National Park (15°45'S 129°05'E); 12727 George Gill Ranges (24°19'S 131°35'E); 13047 Ord River (16°10'S 128°44'E); 15414 Chewings Range (23°40'S 132°54'E); 16473 Sambo Bore, Wave Hill Station (18°53'S 130°40'E); 18042 Alyawarre Desert Area (20°44'S 135°50'E); 20644 Finke Gorge National Park (24°04'30"S 132°40'39"E); 20660 Finke Gorge National Park (24°04'02"S 132°37'36"E); 21128 Carpentaria Highway (16°44'S 135°02'E); 22702 Macdonnell Ranges (24°27'13"S 134°24'59"E); 23764 Gregory National Park (16°49'43"S 130°11'01"E); 23765 Gregory National Park (16°50'20"S 130°10'58"E); 23807 Gregory National Park (16°47'50"S 130°09'15"E); 25495 Jasper Gorge (16°05'50"S 130°45'18"E); 34524-25 Arltunga Ruins (23°26'S 134°42'E).
WAM: 13496 Yirrkala (12°15'S 136°53'E); 21852 8 km N Kalumburu (14°14'S 126°37'E); 21980 Darwin (12°27'S 130°50'E); 23480 Nightcliff (12°23'S 130°52'E); 24001 11 km N Adelaide River (13°08'S 131°08'E); 24198 Helen Springs (18°26'S 133°52'E); 26224 Parap (12°25'S 130°52'E); 28656 Barrow Island (20°50'S 115°25'E); 34331-32 Yirrkala (12°15'S 136°53'E); 37371 Rosemary Island (20°29'S 116°35'E); 37406 Hermite Island (20°29'S 115°31'E); 40296, 40835 Darwin (12°27'S 130°50'E); 41271 Augustus Island (15°19'S 124°32'E); 41370 Heywood Island (15°20'S 124°20'E); 41409 Coronation Island (15°00'S 124°56'E); 43071-75 Crystal Creek (14°31'S 125°48'E); 43119 Port Warrender (14°34'S 125°51'E); 43151, 43185, 43204, 43211, 43341-42 Mitchell Plateau (14°52'S 125°50'E); 44278 Geikie Gorge (18°05'S 125°43'E); 44566-71 Behn River Mouth, Lake Argyle (16°15'S 128°45'E); 44572-75 Ord River (16°17'S 128°47'E); 45066 Napier Range (17°13'S 124°38'E); 48559 Shark Point, Barrow Island (20°52'S 115°25'E); 51277 East Palm Spring, Denison Range (19°20'S 128°20'E); 52670 Lake Argyle (16°07'S 128°44'E); 54141 Edgar Ranges (18°50'S 123°15'E); 56208-09 Crystal Creek (14°30'S 125°47'E); 57039 Doongan Homestead (15°23'S 126°18'E); 60352 3 km E Nicholson (18°03'S 128°55'E); 69845 Koolan Island (16°09'S 123°45'E); 70365 12.5 km 309°New Lissadell Homestead (16°36'12"S 128°27'34"E); 70385 10.5 km 249°New Lissadell Homestead (16°43'S 128°27'E); 70564 5.2 km 202°Mount Percy (17°39'37"S 124°54'24"E); 70582 6.3 km 172°Mount Percy (17°40'23"S 124°56'03"E); 70625 5.2 km 202° Mount Percy (17°39'37"S 124°54'24"E); 75376, 75398 12 km NW New Lissadell Homestead (16°37'S 128°28'E); 75533 11 km WNW New Lissadell Homestead (16°39'S 128°28'E); 77201 Mitchell Plateau (14°44'30"S 125°47'00"E); 77472 Camp Creek (14°53'30"S 125°45'00"E); 79063 Brooking Springs Station (17°54'S 125°16'E); 80028 Sunday Island (16°25'S 123°11'E); 81286 Koolan Island (16°09'S 123°45'E); 94881 Lake Argyle (16°07'S 128°42'E); 96784 Sale River (16°05'S 124°40'E); 96828 Camden Head (15°30'S 124°37'E); 96944 The Dromedaries (16°34'20"S 124°56'40"E); 97091 3.7 km NW Mount Daglish (16°15'05"S 124°56'00"E); 99774, 99776 10 km SW Silent Grove (17°06'55"S 125°10'30"E); 101335 30 km ENE Calwynyardah Homestead (17°57'S 125°02'E); 103120, 103129 Purnululu National Park (17°26'S 128°24'E); 103151 Purnululu National Park (17°33'S 128°15'E); 103207 Purnululu National Park (17°10'S 128°44'E); 103384, 103395 Purnululu National Park (17°15'S 128°18'E); 103483 Purnululu National Park (17°32'S 128°21'E); 103489-90 Purnululu National Park (17°29'S 128°22'E); 103733 Koolan Island (16°09'S 123°45'E); 106284 Augustus Island (15°26'S 124°36'E); 108737 10 km N Gordon Downs Homestead (18°40'S 128°35'E); 108815 30 km SE Gordon Downs Homestead (18°56'S 128°47'E); 112725-26 Mandora Station (19°47'52"S 121°26'53"E); 114462 King Hall Island (16°05'S 123°25'E); 138149 Napier Range (17°13'S 124°38'E); 139058, 139062-63 Mandora Station (19°47'52"S 121°26'53"E); 141530 Quanbun Downs Station (18°21'27"S 125°13'10"E).

Delma pax Kluge 1974
NTM: 9939 24 km N Port Hedland (20°23'S 118°48'E); 9943 13 km N Port Hedland (20°25'S 118°42'E); 9945 15 km N Port Hedland (20°25'S 118°42"E); 9946 22 km N Port Hedland (20°23'S 118°47'E).
WAM: 14803 19 km W Mundabullangana (20°30'S 117°53'E); 51620 10 km NE Mount Newman (23°17'S 119°45'E); 58965 Marble Bar Pool (21°16'S 119°42'E); 64701 Nullagine (21°54'S 120°06'E); 64986 Dampier (20°40'S 116°42'E); 68370-71 Between Nullagine and Roy Hill (22°15'S 120°00'E); 70103 Between Dampier and Karratha (20°45'S 116°45'E); 73144, 73146 24.2 km 234°Marillana Homestead (22°46'00"S 119°13'08"E); 73542-43 Dampier (20°40'S 116°42'E); 73604 24.2 km 234°Marillana Homestead (22°46'00"S 119°13'08"E); 73841 22 km S Roebourne (21°06'S 117°05'E); 76469 10 km SSW Cooya Pooya Homestead (21°07'S 117°07'E); 80379 Carrawella Well (21°43'S 115°31'E); 80599 8 km SE Peedamulla Homestead (21°55'S 115°40'E); 80995-96 South Hedland (20°24'S 118°36'E); 81387-91 Miaree Pool (20°51'S 116°37'E); 82605 Carawine Gorge (21°29'S 121°01'E); 83153 Karratha (20°44'S 116°51'E); 84982 Dampier Archipelago (20°33'S 116°42'E); 87854 Wickham (20°40'S 117°07'E); 90886 Woodstock (21°37'01"S 118°57'13"E); 94660-61 Crossing Pool (21°35'S 117°06'E); 94882 Mardie Station (21°15'S 115°50'E); 102046 2 km N Crossing Pool (20°53'S 116°40'E); 102066 Karratha (20°53'S 116°40'E); 102091 Dampier (20°40'S 116°42'E); 102115 7 km NE Mount Windell (22°37'28"S 118°36'26"E); 102137 5 km NNE Mount Windell (22°36'16"S 118°34'01"E); 102149 10 km ENE Mount Windell (22°35'58"S 118°38'20"E); 104176 Woodstock (21°36'34"S 119°01'17"E); 104297 Woodstock (21°36'25"S 119°02'23"E); 106257, 106278-79, 108711, 108791, 113387 South Hedland (20°24'S 118°36'E); 114437 Wittenoom (22°14'S 118°20'E); 116300 King Bay (20°38'S 116°45'E); 119045-46 South Hedland (20°24'S 118°36'E); 120021 3.5 km NE Mount Brockman (22°28'S 117°18'E); 120030 Hope Downs (22°58'00"S 119°09'45"E); 120735 Boodarie Hill (20°24'S 118°31'E); 125023 Yandicoogina (22°43'S 119°01'E); 125452 30 km E Newman (23°19'S 120°02'E); 127829 Mount Brockman (22°25'05"S 117°18'03"E); 129658 120 km NW Newman (22°59'45"S 119°18'30"E); 129930 West Angelas (23°15'S 118°40'E); 132548 DeGrey River Station

(20°13'14"S 119°09'58"E); 132549 DeGrey River Station (20°17'16"S 119°12'36"E); 132593, 132596 Burrup Peninsula (20°36'45"S 116°47'37"E); 132606 Burrup Peninsula (20°40'49"S 116°44'37"E); 132657 Burrup Peninsula (20°31'40"S 116°49'11"E); 135320, 135336-37 Cape Lambert (20°48'36"S 116°56'31"E); 135632 Bea Bea Creek (21°43'S 118°44'E); 135919-20 32 km SW South Hedland (20°36'S 118°22'E); 137857 Munjina Roadhouse (21°59'S 119°45'E); 139170-71 Cane River Homestead (22°05'19"S 115°37'31"E); 139294 Meentheena (21°17'13"S 120°27'34"E); 139352-53 Potter Island (20°57'S 116°08'E); 139369 Meentheena (21°13'56"S 120°19'40"E); 139457 Mount Minnie Homestead (21°58'23"S 115°25'51"E); 140021 Millstream-Chichester National Park (21°10'53"S 117°03'28"E); 140396 82 km E Port Hedland (20°18'53"S 119°24'41"E); 141269-70 24 km ESE Port Hedland (20°23'S 118°48'E); 141311 Cape Preston area (20°50'00"S 116°09'47"E); 145512 98 km S Port Hedland (21°09'36"S 118°48'36"E); 145544 80 km S Port Hedland (21°00'36"S 118°42'00"E); 145569 34 km S Port Hedland (20°36'36"S 118°36'36"E); 145614 18 km S Port Hedland (20°28'12"S 118°35'24"E); 145680 Abydos Station (21°25'S 118°55'E); 145748 Chichester Range (22°04'44"S 118°58'40"E); 145753 Chichester Range (22°01'01"S 118°58'55"E); 146591 124 km S Port Hedland (21°26'53"S 118°55'24"E); 146649 80 km S Port Hedland (21°00'36"S 118°42'00"E); 151161 Tom Price area (22°37'13"S 117°44'37"E).

Delma tincta De Vis 1888

WAM: 3440 La Grange (18°40'S 122°01'E); 4511 East Chapman (28°40'S 114°50'E); 8109 Wandagee Station (23°49'S 114°27'E); 9782-84 Carnarvon (24°53'S 113°40'E); 10615 Minilya (23°51'S 113°58'E); 11494 Learmonth district (22°15'S 114°05'E); 12114 Kimberley Research Station (15°39'S 128°42'E); 13653 Wyndham (15°29'S 128°07'E); 13838 Kalumburu (14°18'S 126°38'E); 13933 Mount Pleasant * (32°02'S 115°51'E); 14791-95 Northampton (28°21'S 114°38'E); 14801 Mundabullangana (20°31'S 118°03'E); 17683 Turee Creek Station (23°37'S 118°39'E); 22323 Nabawa (28°30'S 114°47'E); 22366 Kimberley Research Station (15°39'S 128°42'E); 24812 Binnu (28°02'S 114°40'E); 25221 Murchison House (27°39'S 114°14'E); 28370 Coordewandy (25°36'S 115°58'E); 28391 Murchison House (27°39'S 114°14'E); 28454 Barrow Island (20°48'S 115°24'E); 30259 Carnarvon (24°53'S 113°40'E); 31397 35 km NE Mingenew (29°03'S 115°37'E); 31487 Eradu (28°42'S 115°02'E); 44555-65 Lake Argyle (16°10'S 128°44'E); 47854 Barrow Island (20°52'S 115°22'E); 48560-62 Barrow Island (20°52'S 115°25'E); 50091 Yalgoo (28°21'S 116°41'E); 51003-04 Exmouth (21°56'S 114°07'E); 51641 Marandoo (22°38'S 118°08'E); 52933 Shothole Canyon (22°03'S 114°02'E); 53791-93 Gascoyne Junction area (25°06'S 115°13'E); 54606 Wooramel Homestead (25°44'S 114°17'E); 55019 Hamelin Homestead (26°26'S 114°12'E); 55094 Wooramel Homestead (25°44'S 114°17'E); 55406-07, 55440 71 km W Barry Caves (19°52'S 136°03'E); 58413 5 km N Coulomb Point (17°19'S 122°10'E); 59687, 59689 Meeberrie Homestead (26°58'S 115°58'E); 62208 Mingenew (29°12'S 115°26'E); 62416 5 km W Williambury Homestead (23°54'S 115°10'E); 63678 25 km NNW Winning Homestead (22°56'S 114°27'E); 66313 36 km 137°Mount Meharry (23°12'30"S 118°49'30"E); 66314 34 km 136°Mount Meharry (23°11'40"S 118°49'30"E); 66327 36 km 137°Mount Meharry (23°12'30"S 118°49'30"E); 67606-09 Marble Bar (21°10'S 119°44'E); 67806 Hamelin Pool (26°24'S 114°10'E); 67905 36 km 137°Mount Meharry (23°12'30"S 118°49'30"E); 69779 Mount Bruce (22°35'S 118°10'E); 70757, 70761, 70764 30.2 km 238°Marillana Homestead (22°46'55"S 119°09'35"E); 71059 Hamelin Homestead (26°26'S 114°12'E); 73138 30.2 km 238°Marillana Homestead (22°46'58"S 119°09'35"E); 73897 Pender Bay area (16°45'S 122°49'E); 78239 70 km W Barry Caves (19°51'S 136°02'E); 81330 57 km NNE Nanutarra Roadhouse (22°01'S 115°36'E); 83152 Karratha (20°44'S 116°51'E); 83210 Carnarvon (24°53'S 113°40'E); 84150-52 Yalgoo (28°21'S 116°41'E); 85190 8 km ESE Kununurra (15°49'S 128°48'E); 86429 Hamelin Homestead (26°26'S 114°12'E); 88547 Carnarvon (24°53'S 113°40'E); 91132 10 km NE Paynes Find (29°11'S 117°42'E); 92727 Hamelin Homestead (26°26'S 114°12'E); 93701 53 km NNE Broome (17°32'S 122°25'E); 95291-93 Walga Rock (27°24'S 117°28'E); 99180 Woodstock Station (21°36'35"S 118°57'44"E); 101246 Galena (27°50'S 114°41'E); 101278 Barrow Island (20°48'S 115°24'E); 102154 10 km ENE Mount Windell (22°35'58"S 118°38'20"E); 102401 Barlee Range Nature Reserve (23°04'47"S 115°47'14"E); 102815 Burrup Peninsula (20°40'39"S 116°45'11"E); 102838 Cape Range National Park (22°09'01"S 113°59'52"E); 102852 Meentheena (21°14'16"S 120°23'31"E); 139140 Meentheena (21°25'18"S 120°25'36"E); 104426, 105987 Carnarvon (24°53'S 113°40'E); 112511 Urala Station (21°47'04"S 114°52'07"E); 112689 10 km SSW Onslow (21°43'51"S 115°05'49"E); 112690 5.5 km SE Onslow (21°40'33"S 115°08'42"E); 112691 11 km S Onslow (21°44'27"S 115°06'46"E); 112715 5.5 km SE Onslow (21°40'33"S 115°08'42"E); 112716 12 km SE Onslow (21°42'39"S 115°11'49"E); 112747 Bibawarra Crossing (24°53'S 113°42'E); 113012, 113030 Lesley Salt Works (20°14'50"S 118°50'50"E); 114101-02 Carnarvon Airport (24°54'S 113°39'E); 114391-92 9 km NE Broome (17°55'S 122°15'E); 114490 Wicherina Dam (28°44'S 115°00'E); 115018 Spalding Park (28°39'S 114°38'E); 116439 15 km NNW Carlton Hill Homestead (15°23'39"S 128°28'13"E); 116545 Depot Hill (29°08'S 115°21'E); 117215 Narngulu (28°49'S 114°41'E); 117342 Hope Downs (22°56'45"S 119°07'30"E); 120020 3.5 km NE Mount Brockman (22°28'S 117°18'E); 125032 Yandicoogina (22°43'14"S 118°59'26"E); 127718, 127768, 127792 5 km S Mount Tom Price Mine (22°47'55"S 117°46'10"E); 129587, 129623 120 km NW Newman (22°55'S 118°54'E); 131752 Mount Robinson (22°57'19"S 118°46'14"E); 132209 Urala Station (21°47'09"S 114°51'58"E); 135322 Cape Lambert (20°45'16"S 117°04'52"E); 135422 Mount Brockman (22°18'38"S 117°15'08"E); 135487 Urala Station (21°46'58"S 114°52'11"E); 137953 35 km NNE Kununurra (15°35'20"S 128°59'00"E); 138222 Karijini National Park (22°37'S 118°17'E); 138226 Karijini National Park (23°01'S 118°43'E); 138243 Karijini National Park (22°59'S 118°44'E); 139140 Meentheena (21°25'18"S 120°25'36"E); 139282 Meentheena (21°17'07"S 120°24'55"E); 139308 Meentheena (21°14'41"S 120°19'20"E); 139314 Meentheena (21°13'04"S 120°27'20"E); 139321 Meentheena (21°15'20"S 120°27'18"E); 139328 Meentheena (21°16'54"S 120°27'58"E); 141273 22 km ESE Port Hedland (20°23'S 118°47'E); 141584 1 km N Quobba Homestead (24°22'24"S 113°24'19"E); 141585-86 Quobba Station (24°27'42"S 113°24'28"E); 145250 5 km S Mount Tom Price Mine (22°48'31"S 117°47'09"E); 145650 235 km SSW Port Hedland (22°23'24"S 118°58'48"E); 146589, 146645 228 km SSW Port Hedland (22°20'24"S 119°00'00"E); 146890 Mirima National Park (15°47'S 128°44'E); 146957 Kalumburu (14°18'S 126°38'E); 151059-60 10 km E

Carnarvon (24°53'S 113°46'E); 153814 2 km S Yardie Homestead Caravan Park (21°53'37"S 114°00'34"E); 153820 Charles Knife Road (22°07'08"S 114°03'44"E); 153821 Bullara Station (22°48'33"S 113°56'39"E).
*As noted by Kluge (1974), this locality record is considered erroneous.

Delma sp. *incertae sedis*
SAM: 5058 Warburton Range (26°06'S 126°39'E); WAM: 25201 32 km E Jiggalong (23°22'S 121°05'E).

Specimens examined in allozyme analysis

Delma pax
WAM: 104297 Woodstock Station; 120021 3.5 km NE Mount Brockman; 120030 Hope Downs; 125452 30 km E Newman; 132548 De Grey River Station; 132596, 132606 Burrup Peninsula; 135920 South Hedland; 139171 Cane River Homestead; 139294 Meentheena; 140021 Millstream-Chichester National Park; 141270 24 km ESE Port Hedland.

Delma desmosa sp nov.
WAM: 102650, 102657 Little Sandy Desert; 114555 Sandfire Roadhouse; 132802 Warri Airstrip; 139089 Mandora; 145073 Officer Basin area.

Delma tealei sp nov.
WAM: 102837 Cape Range National Park; 153811 Charles Knife Road; 153813 2 km S Yardie Homestead Caravan Park; 153819 Shothole Canyon.

Delma borea
WAM: 139058, 139063 Mandora; 141530 Quanbun Downs Station.

Delma tincta
WAM: 102401 Barlee Range Nature Reserve; 102838 Cape Range National Park; 114391 9 km NE Broome.

Delma butleri
"western"
WAM: 120819 Peron Peninsula (26° 00'S 113° 30'E); 141590 Boolathana Station (24° 39'S 113° 42'E); 127461 East Yuna Nature Reserve (28° 20'S 115° 00'E); 144711 Bungalbin Hill (30° 24'S 119° 38'E).

"central"
WAM: 106163 Mount Frazer (25° 38'S 118° 23'E); 135249 Wiluna (26° 35'S 120° 14'E); 145072 Officer Basin (29° 58'S 123° 46'E).
SAM: 35027 Bloodweed Bore (26° 57'S 140° 57'E).

"eastern"
SAM: 45210 Peebinga Conservation Park (34° 58'S 140° 50'E).

Delma haroldi
WAM: 102123 Mount Windell (22° 39'S 118° 33'E); 135924 Sandfire Roadhouse (19° 46'S 121° 05'E); 145653 Port Hedland (20° 18'S 118° 35'E); NTM: 16484 Wave Hill Station (17° 29'S 130° 57'E).

APPENDIX 2

Allozyme profiles for 41 specimens at 34 variable loci

Legend for Museum registration numbers: WAM = Western Australian Museum; NTM = Northern Territory Museum; SAM = South Australian Museum; (c) = "central"; (w) = "western"; (e) = "eastern". A dash indicates the enzyme lacked sufficient activity to determine a profile.

Species	Accession Number	*Acon1*	*Acon2*	*Acp1*	*Acp2*	*Acyc*	*Ada*	*Adh1*	*Adh2*	*Ca*	*Dia*	*Enol*	*Est2*	*Fdp*	*Fum*	*Gda*	*Glo*	*Got1*	*Got2*	*Gpd*	*Gpi*	*Guk*	*Idh2*	*Mei*	*Mpi*	*Ndpk1*	*Ndpk2*	*Pepa*	*Pepb*	*Pepd*	*6Pgd*	*Pgm1*	*Pgm2*	*Sod*	*Srdh*
pax	WAM104297	a	d	a	b	ab	b	b	d	a	b	c	d	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	ef	cd	b	c	a	d	b
pax	WAM120021	a	d	a	b	b	b	b	d	a	bc	c	de	c	b	c	c	b	b	b	b	ab	c	c	b	a	b	b	f	c	bc	c	a	d	ab
pax	WAM120030	a	d	a	b	b	b	b	d	a	e	c	d	c	b	c	c	b	a	b	b	b	c	c	b	a	b	b	f	cd	b	c	a	d	b
pax	WAM125452	a	d	a	b	a	b	b	d	a	bc	c	de	c	b	c	c	b	a	b	b	ab	c	c	b	a	b	b	f	d	bc	c	a	dg	ab
pax	WAM132548	a	d	a	b	a	b	b	d	a	b	c	d	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	f	cd	b	c	a	d	b
pax	WAM132596	a	bd	a	b	ab	b	b	d	a	b	c	de	c	b	c	c	b	b	b	b	b	c	c	b	a	b	bc	f	cd	b	c	a	d	b
pax	WAM132606	a	d	a	b	ab	b	b	d	a	b	c	de	c	b	c	c	b	b	b	b	ab	c	c	b	a	b	c	f	c	bc	c	a	d	b
pax	WAM135920	a	d	a	b	ab	b	b	d	a	b	c	d	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	f	c	b	c	a	d	b
pax	WAM139171	a	d	a	b	b	b	b	d	a	b	c	e	c	b	c	c	b	b	b	b	b	c	c	b	a	b	b	f	cd	b	c	a	d	b
pax	WAM139294	a	d	a	b	b	b	b	d	a	e	c	de	c	b	c	c	b	b	b	b	ab	c	c	b	a	b	c	f	cd	b	c	a	d	b
pax	WAM140021	a	d	a	b	ab	b	b	d	a	bc	c	e	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	f	cd	b	c	a	d	b
pax	WAM141270	a	d	a	b	b	b	b	d	a	b	c	d	c	b	c	bc	ab	b	b	b	a	c	c	b	a	b	c	f	d	b	c	a	d	b
desmosa	WAM102650	a	c	a	b	b	b	c	a	a	ab	c	d	c	b	c	ac	b	a	b	b	b	c	c	b	a	b	c	df	d	b	b	a	d	b
desmosa	WAM102657	a	cd	a	b	b	b	c	ac	a	b	c	d	c	b	c	c	b	a	b	b	b	c	c	b	a	b	c	f	cd	b	bc	a	d	b
desmosa	WAM114555	a	cd	a	b	b	b	b	c	a	–	c	–	c	b	c	c	b	a	–	ab	b	c	a	b	a	b	c	f	cd	b	–	a	d	–
desmosa	WAM132802	a	cd	a	b	b	b	bc	ac	a	b	c	d	c	b	c	c	b	a	–	b	b	c	c	b	a	b	c	f	cd	b	c	a	d	b
desmosa	WAM139089	a	cd	a	b	b	b	c	c	a	a	c	d	bc	b	c	ac	b	a	b	b	b	c	a	b	a	b	c	f	c	b	c	a	d	b
desmosa	WAM145073	a	c	a	b	b	bc	c	a	a	b	c	d	c	b	c	c	b	a	b	b	b	c	c	b	a	c	c	f	d	b	c	a	d	b

Appendix 2 (cont.)

Species	Accession Number	*Acon1*	*Acon2*	*Acp1*	*Acp2*	*Acyc*	*Ada*	*Adh1*	*Adh2*	*Ca*	*Dia*	*Enol*	*Est2*	*Fdp*	*Fum*	*Gda*	*Glo*	*Got1*	*Got2*	*Gpd*	*Gpi*	*Guk*	*Idh2*	*Me1*	*Mpi*	*Ndpk1*	*Ndpk2*	*PepA*	*PepB*	*PepD*	*6Pgd*	*Pgm1*	*Pgm2*	*Sod*	*Srdh*
tealei	WAM102837	a	c	a	b	a	b	b	c	a	hj	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	c	b	e	a	d	b
tealei	WAM153811	a	c	a	b	a	b	b	c	a	h	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	c	b	e	a	d	b
tealei	WAM153813	a	c	a	b	a	b	b	c	a	h	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	c	b	e	a	d	b
tealei	WAM153819	a	c	a	b	a	b	b	c	a	h	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	ac	ab	e	a	d	b
borea	WAM139058	a	c	b	b	a	b	b	c	a	h	c	bc	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	cd	b	g	a	c	b
borea	WAM139063	a	c	b	b	a	b	b	c	a	h	c	bc	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	cd	b	g	ab	c	b
borea	WAM141530	a	cd	b	b	a	b	b	c	a	dg	c	b	a	b	d	c	b	b	b	b	ab	c	c	b	a	ab	c	e	df	b	g	a	c	b
tincta	WAM102401	a	ac	a	a	a	bd	b	a	a	gh	c	–	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	d	b	d	a	d	d
tincta	WAM102838	a	bc	a	a	a	bd	b	a	a	g	c	ab	a	b	d	c	b	b	a	b	a	c	c	b	a	b	c	e	bd	c	d	a	d	d
tincta	WAM114391	a	b	a	a	b	b	b	a	a	g	c	b	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	d	b	d	a	d	b
butleri (c)	WAM106163	b	d	a	a	a	b	b	bc	b	fi	c	b	a	bd	c	d	b	c	b	c	a	b	b	a	b	b	c	be	d	d	e	a	d	c
butleri (w)	WAM120819	b	a	a	a	a	b	–	c	b	–	ac	–	–	b	c	d	b	c	–	c	a	ab	b	a	b	b	ac	e	d	d	–	a	–	b
butleri (w)	WAM127461	bc	a	a	a	a	b	–	c	b	g	c	b	a	bd	c	d	b	c	b	c	a	b	c	a	b	b	c	be	cd	d	a	a	d	c
butleri (c)	WAM135249	b	d	a	a	a	b	b	b	b	fh	c	b	a	b	c	d	b	c	–	c	a	b	b	a	b	b	c	e	d	d	e	a	d	c
butleri (w)	WAM141590	b	a	a	a	a	b	b	c	b	–	b	b	a	b	ac	d	b	c	b	c	a	b	b	a	b	b	c	e	cd	d	c	a	d	b
butleri (w)	WAM144711	b	ab	a	a	a	b	–	c	b	gi	c	b	a	b	c	d	b	c	–	c	a	b	b	a	b	b	c	be	df	d	c	a	d	c
butleri (c)	WAM145072	a	d	a	a	a	b	b	c	b	gj	c	b	a	b	c	d	b	c	b	c	a	b	b	a	b	bd	c	be	d	d	e	a	ad	c
butleri (e)	SAM45210	b	de	a	a	a	b	b	c	b	g	c	b	a	bc	c	d	c	c	b	c	a	b	b	a	b	b	d	a	cd	e	f	a	d	c
butleri (c)	SAM35027	a	d	a	a	a	b	ab	b	b	c	c	b	a	b	c	d	b	c	b	c	a	b	b	a	b	b	c	be	d	d	ef	a	ad	c
haroldi	WAM102123	a	a	a	a	a	b	b	b	b	–	b	b	a	bd	c	d	b	c	b	c	a	ab	c	a	b	b	c	ac	dg	d	e	a	a	c
haroldi	WAM135924	ab	d	a	a	a	b	b	b	b	–	c	b	a	ab	c	d	b	c	b	c	a	b	c	a	b	b	c	b	df	d	e	a	a	c
haroldi	WAM145653	a	c	a	a	ac	ab	b	b	b	–	c	b	a	b	c	d	b	c	b	c	a	b	bc	a	b	b	c	be	de	d	e	a	bf	c
haroldi	NTM16484	ab	ad	a	a	ac	b	b	b	b	–	c	bc	a	b	bc	d	b	d	b	c	a	bd	c	a	b	b	c	be	d	d	ef	a	be	c

Records of the Western Australian Museum **23**: 307–308 (2007). **Short communication**

First record of the freshwater sawfish, *Pristis microdon*, from southwestern Australian waters

Justin A. Chidlow

Department of Fisheries, Western Australian Marine Research Laboratories,
PO Box 20, North Beach, Western Australia 6920
Email: jchidlow@fish.wa.gov.au

Sawfishes (family Pristidae) are large (up to 7m) modified batoids with a blade-like snout edged with pairs of rostral teeth. They occur worldwide in sub-tropical and tropical shallow coastal sea, estuaries and freshwater systems (Last and Stevens 1994; Compagno and Last 1998). There are between five and seven recognised species worldwide, with five species represented in Australian waters (Last and Stevens 1994). Sawfish populations have been extirpated from many parts of their original global range by gillnetting and trawling and are easily entangled in nets by their toothed rostra (Simpfendorfer 2000). The little that is known about the biology of sawfish suggests they have low rates of reproduction (Tanaka 1991; Compagno and Last 1998; Wilson 1999; Simpfendorfer 2000; Thorburn *et al.* 2004). This combined with their susceptibility to fishing gear, make sawfish a high risk species and all have subsequently been listed globally as critically endangered under the IUCN Red List Assessment 2006 (Compagno *et al.* 2006).

Pristis microdon **Latham, 1794**

Pristis microdon is a medium to large sawfish that in Australia grows to at least 361cm TL (Tanaka 1991), but is reported to reach up to 700cm TL in other locations (Last and Stevens 1994). They are born at around 50cm in length after a five month gestation period, with litter sizes ranging between 1 and 12 (Wilson 1999). In the western Atlantic *P. microdon* matures at between 240cm and 300cm TL (Compagno and Last 1998). Tanaka (1991) reported two male specimens from New Guinea, one measuring 247cm that was immature and a 361cm specimen that was mature. In Australian waters, *P. microdon* feeds on fish such as catfish, small crustaceans and molluscs (Allen 1982; Cliff and Wilson 1994; Pogonoski *et al.* 2002; Thorburn *et al.* 2004).

Pristis microdon occurs inshore and in intertidal areas and is usually found in freshwater drainages, lakes and estuaries where it can penetrate as far as 400km from the coast (Morgan *et al.* 2004). In the Indo-West Pacific it ranges from New Guinea, SE Asia, northern Australia and west to South Africa (Last and Stevens 1994; Compagno and Last 1998). *Pristis microdon* may also occur in the Atlantic and eastern Pacific if *P. perotteti* Müller & Henle, 1841 and *P. zephyreus* Jordan & Starks in Jordan, 1895 are synonymised with this species (Compagno and Last 1998). In Australia, the freshwater sawfish is known to occur in the Ord, Durack and Fitzroy Rivers (Western Australia), the Adelaide, Victoria and Daly Rivers (Northern Territory), and the Gilbert, Mitchell, Norman and Leichhardt Rivers (Queensland) (Last and Stevens 1994; Pogonoski *et al.* 2002; Thorburn *et al.* 2004). Only recently has *P. microdon* been reported from marine waters (Thorburn *et al.* 2004).

Southwestern Australian *P. microdon*

A female *P. microdon* was captured by a commercial shark fisher operating demersal gillnets in southwestern Australian waters on the 5th of February 2003. The capture location was approximately six miles east of Cape Naturaliste (33°31'S, 115°07'E) in 32m of water. The sawfish was estimated to be 3.5m in length TL when landed and appeared to be healthy. The specimen was processed and the fisher retained the remaining trunk, fins and saw. I positively identified the processed sawfish as *P. microdon* using an identification key provided by Last and Stevens (1994).

The partial length (origin of the first dorsal fin to the insertion point of the second dorsal fin) was 95cm (approximate as the trunk had been cut in half). The rostral saw length was 79cm with 19 pairs of teeth that extended to the basal quarter of the saw (Figure 1). The interspace between rostral teeth at the base of the saw was 4cm, and 3cm between the teeth at the tip of the saw (Figure 1). A groove was present along the posterior margin of all rostral teeth. The origin of the first dorsal-fin was located anterior to the pelvic-fin origin and the height of the first dorsal-fin was 32cm. The second dorsal-fin height was 31cm. The ventral lobe of the caudal-fin was small, but distinct. The upper and lower postventral caudal-fin margins measured 44.5cm and 11.5cm respectively.

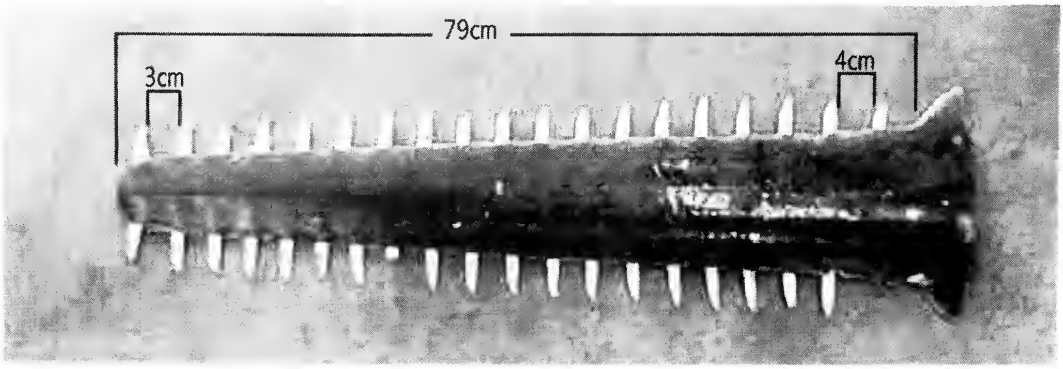


Figure 1 Rostral saw from a female *Pristis microdon*, measuring approximately 350cm in total length, captured off Cape Naturaliste, Western Australia. See text for description of measurements.

This record of *P. microdon* from southwestern Australia extends the range of the species approximately 1600 km south of its previously known southern limit, Cape Keraudren, Western Australia (Thorburn *et al.* 2004) and provides further confirmation that *P. microdon* utilizes marine waters.

ACKNOWLEDGEMENTS

I wish to thank J. Nelson who thoughtfully informed the Shark Research Section, Department of Fisheries WA of the capture, and provided assistance in identifying and collecting data from the specimen. I would also like to thank P. Last from CSIRO Marine Research, Hobart, R. McAuley from Department of Fisheries WA, Perth and C. Simpfendorfer from the Mote Marine Laboratory, Florida for their assistance in positively identifying the specimen.

REFERENCES

Allen, G.R. (1982). *A field guide to inland fishes of Western Australia*. Western Australian Museum, Perth, Western Australia. 86pp.

Cliff, G. and Wilson, G. (1994). Natal sharks board's guide to sharks and other marine animals. *Natal Sharks Board*, p33.

Compagno, L.J.V. and Last, J.D. (1999). Pristiformes: Pristidae. *In* K.E. Carpenter and V.H. Niem (eds). *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae)*. Pp. 1410–1417. FAO, Rome.

Compagno, L.J.V., Cook, S.F. and Fowler, S.L. (2006). *Pristis microdon*. *In* IUCN 2006 IUCN Red List of Threatened Species.

Jordan, D.S. and Starks, E.C. (1895). *In* The fishes of Sinaloa. D.S. Jordan. Proceedings of the Califfornia Academy of Sciences (Ser. 2) 377–514.

Last, P.R. and Stevens, J.D. (1994). *Sharks and rays of Australia*. CSIRO, Melbourne, 513 pp.

Latham, J. (1794). An essay on the various species of sawfish. *Transactions of the Linnean Society of London* **2** (25): 273–282.

Morgan, D.L., Allen, M.G., Bedford, P. and Horstman, M. (2004). Fish fauna of the Fitzroy River in the Kimberley region of Western Australia – including Bunuba,Gooniyandi, Ngarinyin, Nyikina and Walmajarri Aboriginal names. *Records of the Western Australian Museum* **22**:147–161.

Müller, J and Henle, F.G.J. (1841). Systematische Beschreibung der Plagiostomen Berlin. Plagiostomen i–xxii + 1–200.

Pogonoski, J.J., Pollard, D.A. and Paxton, J.R. (2002). Conservation overview and action plan for Australian threatened and potentially threatened marine and estuarine fishes. *Environment Australia*, February 2002.

Simpfendorfer, C.A. (2000). Predicting population recovery rates for endangered western Atlantic sawfishes using demographic analysis. *Environmental Biology of Fishes* **58**: 371–377.

Tanaka, S. (1991). Age estimation of freshwater sawfish and sharks in northern Australia and Papua New Guinea. The University Museum, University of Tokyo. *Nature and Culture* **3**: 71–82.

Thorburn, D., Morgan, D., Gill, H., Johnson, M., Wallace-Smith, H., Vigilante, T., Gorring, A., Croft, I. and Fenton, J. (2004). Biology and cultural significance of the freshwater sawfish (*Pristis microdon*) in the Fitzroy River, Kimberley, Western Australia. *Report to the Threatened Species Network* 2004. 57 pp.

Thorson, T.B. (1982). The impact of commercial exploitation on sawfish and shark populations in Lake Nicaragua. *Fisheries* 7(2): 2–10.

Wilson, D. (1999). Freshwater sawfish *Pristis microdon*. Australia New Guinea Fishes Associations' A-Z notebook of native freshwater fish. *ANGFA Bulletin* **41**.

Manuscript received 23 August 2004; accepted 3 August 2006

Guide to Authors

Subject Matter:

Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

Presentation:

Authors are advised to follow the layout and style in the most recent issue of the *Records of the Western Australian Museum* including headings, tables, illustrations and references.

The title should be concise, informative and contain key words necessary for retrieval by modern searching techniques. An abridged title (not exceeding 50 letter spaces) should be included for use as a running head.

An abstract must be given in full length papers but not short communications, summarizing the scope of the work and principal findings. It should normally not exceed 2% of the paper and should be suitable for reprinting in reference periodicals.

The International System of units should be used.

Numbers should be spelled out from one to nine in descriptive text; figures used for 10 or more. For associated groups, figures should be used consistently, e.g., 5 to 10, not five to 10.

Spelling should follow the *Concise Oxford Dictionary*.

Systematic papers must conform with the International Codes of Botanical and Zoological Nomenclature and, as far as possible, with their recommendations.

Synonymies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper. All citations, including those associated with scientific names, must be included in the references.

Manuscripts:

The original and two copies of manuscripts and figures should be submitted to the Editor, c/- Publications Department, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus heading and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

High quality illustrations are required to size (16.8 cm x 25.2 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, not exceeding 16.8 cm x 25.2 cm. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance a computer disk containing all corrections should be sent with amended manuscript. The disk should be marked with program (e.g. Word, WordPerfect, etc).

In papers dealing with historical subjects references may be cited as footnotes. In all other papers references must be cited in the text by author and date and all must be listed alphabetically at the end of the paper. The names of journals are to be given in full.

Processing:

Papers and short communications are reviewed by at least two referees and acceptance or rejection is then decided by the editor.

The senior author is sent one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

Records of the Western Australian Museum
Volume 23 Part 3 2007

CONTENTS